A New Genus and Species of Pygmy Pipehorse from Taitokerau Northland, Aotearoa New Zealand, with a Redescription of Acentronura Kaup, 1853 and Idiotropiscis Whitley, 1947 (Teleostei, Syngnathidae)

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Cylix tupareomanaia, new genus and species, is described from three specimens (35.5–55.5 mm SL), collected from rocky reefs at 12–17 m depth from Taitokerau Northland, New Zealand. The new taxon shares morphological synapomorphies with the superficially similar Australian endemic Idiotropiscis and Indo-Pacific Acentronura, including head angled ventrally approximately 25° from the principal body axis, enclosed brood pouch, brood pouch plates, prehensile tail, and absence of caudal fin. Cylix tupareomanaia, new genus and species, however, is distinguishable from all other members of the Syngnathidae by the following combination of bony autapomorphic characters: a cup-like crest present anterodorsally on the supraoccipital; and large conspicuous midventral conical spines on the cleithral symphysis and first trunk ring between the pectoral-fin bases. The new species can be further differentiated by genetic divergence in the mitochondrial COX1 gene from Acentronura breviperula, A. tentaculata, Idiotropiscis australae, and I. lummitzeri (estimated uncorrected p-distances of 19.5%, 20.4%, 17.9%, and 18.4%, respectively). A phylogenetic hypothesis from the analysis of two nuclear loci, 18S and TMO-4C4, supports the placement of C. tupareomanaia, new genus and species, as the sister taxon to a clade comprising the genera Acentronura and Idiotropiscis. Cylix tupareomanaia, new genus and species, represents the eighth member within the pygmy pipehorse clade to be described from the Indo-Pacific and the first new genus and species of syngnathid to be reported from New Zealand since 1921.

SYNGNATHIDAE is a large and morphologically distinctive group of predominantly marine fishes, with 57 genera and 300 described species that include the seahorses, pipefishes, pygmy pipefishes, and seadragons (Dawson, 1985; Hamilton et al., 2017; WoRMS Editorial Board, 2021). Syngnathids primarily inhabit shallow coastal waters in temperate and tropical oceans, and are characterized by male brooding, a unique overall body plan, including an elongated snout, fused jaw, the absence of pelvic fins, and absence of caudal fin. The inshore marine ichthyofauna of New Zealand includes a small but diverse group of syngnathids represented by ten species in five genera: Hippocampus, Leptonotus, Lissocampus, Solegnathus, and Stigmatopora (Dawson, 1980, 1985; Roberts et al., 2015; Clark et al., 2017). Four species of syngnathids are endemic to New Zealand, including Lissocampus filum, a kelp-associated species, Stigmatopora macropterygia, the largest member of its genus, and two uncommon sand and rubble-associated species, Leptonotus elevatus and L. norae, that belong to a Pacific genus with a disjunct distribution with the only other species, L. blainvilleanus, occurring in South America. In contrast, syngnathid diversity in nearby Australia is exceptionally high with 129 species represented in 47 genera, 11 of which are monotypic (Dawson, 1985; Browne et al., 2008; Baker et al., 2009; Hamilton et al., 2017). All genera of syngnathids that occur in temperate mainland New Zealand, with the exception of Leptonotus, occur in southern Australia (Dawson, 1985). Similarly, New Caledonia, which is linked to New Zealand by the almost entirely submerged continental landmass Te Riu-a-Māui Zealandia (Mortimer et al., 2017), exhibits high syngnathid diversity and endemism with 41 species in 14 genera (Fricke et al., 2011).

Recent surveys of inshore marine biodiversity at the offshore subtropical Rangitāhua Kermadec Islands in the northernmost region of New Zealand produced new records of Indo-Pacific syngnathids (Francis and Duffy, 2015; Trnski et al., 2015; Clark et al., 2017). These surveys yielded the

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Submitted: 5 October 2020. Accepted: 15 March 2021. Associate Editor: M. T. Craig.

© 2021 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/i2020136 Published online: 20 September 2021
pipfish species *Cosmocampus howensis*, *Halicampus boothae*, and the rare southwest Pacific seahorse *Hippocampus jugumus*, all of which were originally described based on specimens collected from Lord Howe Island, Australia (Whitley, 1948; Allen et al., 1976; Smith et al., 2010). In 2009 and 2014, the Bay of Islands Coastal Survey Project, coordinated by the National Institute of Water and Atmospheric Research (NIWA), conducted extensive marine biodiversity surveys of shallow water coastal habitats in the Northland region of New Zealand, including the Bay of Islands and the Cavalli Islands. These surveys each yielded two individuals of a diminutive syngnathid (Jones et al., 2009; NIWA, 2014: https://niwa.co.nz/news/rare-fish-and-new-seafloor-habitats-found-during-niwa-survey-of-coastal-east-northland) that were provisionally identified as the Australian pygmy pipehorse *Idiotropiscis australis* based on a superficial similarity to this species (Stewart, 2015).

Members of the genus *Idiotropiscis* belong to a grouping of Indo-Pacific species of pygmy pipehorses comprising the genera *Acentronura* and *Kyonemichthys*, all of which have the head angled slightly ventrally from the abdominal axis, a fully enclosed male brood pouch, prehensile tail, and no caudal fin. The Western Atlantic pygmy pipehorse genus *Amphelikkturus* appears to have evolved independently in the Atlantic to the extent that Dawson (1984) suggested all pygmy pipehorses shared a common ancestor; however, molecular and morphological differences support the findings of independent evolution of Atlantic and Pacific pygmy pipehorses (Hamilton et al., 2017). A multi-gene phylogenetic hypothesis of relationships of the family Syngnathidae recovered *Acentronura* and *Idiotropiscis* as sister taxa within a clade of highly morphologically distinct Indo-Pacific pipefish genera *Filicampus*, *Trachyrhamphus*, *Haliichthys*, and *Lissocampus* (Hamilton et al., 2017). Even though *Acentronura* and *Idiotropiscis* share the synapomorphy of fully enclosed brood pouch, prehensile tail, and absence of caudal fin with the seahorse genus *Hippocampus*, no immediate sister taxon relationship was supported among these genera (Hamilton et al., 2017). Instead, a sister-group relationship was recovered between the Indo-Pacific clade containing *Acentronura* and *Idiotropiscis* and a globally distributed and well-defined clade of seahorses (Hamilton et al., 2017). The three previously described species of the genus *Idiotropiscis*, *I. australis* (type species of the genus), *I. larsonae*, and *I. lummitzeri*, are endemic to the shallow coastal waters of Australia (Waite and Hale, 1921; Dawson, 1984; Kuiter, 2004). *Idiotropiscis australis* occurs in South Australia and southern Western Australia, *I. larsonae* in northern Western Australia, and *I. lummitzeri* in southern New South Wales.

Although the collected specimens from northern New Zealand appeared superficially similar in appearance to *I. australis* based on shared synapomorphies, such as the head angled ventrally approximately 25° from the principal body axis, a fully enclosed brood pouch, brood pouch plates, prehensile tail, and absence of caudal fin (Stewart, 2015), closer investigation revealed a number of unique morphological characters present on the head that differed markedly from *I. australis*, and with features unknown from any other species of pygmy pipehorse described previously. On the basis of these morphological features, molecular sequence data, and phylogenetic analysis, we consider the species from Taitokerau, Northland, New Zealand as a new genus and species of pygmy pipehorse in the family Syngnathidae, and we describe it herein. Non-type representatives of the superficially similar *Acentronura* and *Idiotropiscis* are redescribed based on a substantially expanded dataset of morphological characters (compared to the original descriptions), as revealed by micro-computed tomography. Comparisons of these morphological characters revealed novel species-specific neurocranial characters that assisted in the identification of the generic limits of *Acentronura*, *Idiotropiscis*, and *Cylix*, new genus.

**MATERIALS AND METHODS**

**Morphological analyses.**—Head and body measurements reported follow Short et al. (2018) and are expressed as percent of standard length (SL) or head length (HL). Osteocranial and postcranial skeletal terminology follows Lyeisen (2011). External morphological characters were documented using a dissecting microscope and analyses of high-resolution digital images. Morphological characters of the axial skeleton of type specimens and comparative material were examined via non-destructive x-ray microcomputed tomography (µCT) at the Karel F. Liem Bioimaging Facility (Friday Harbor Laboratories, University of Washington). Micro-computed tomography (µCT) was performed using a Bruker Skyscan 1173 scanner (Billerica, MA) with a 1 mm aluminum filter at 60 kV and 110 µA on a 2048 x 2048 pixel CCD at a resolution of 8.8 lm. The specimens were placed inside a 50 ml plastic Falcon tube (Corning, NY), supported by two thin foam pads to prevent movement during scanning and wrapped in 70% ethanol-infused cheesecloth to maintain moist conditions and prevent desiccation. The resulting µCT data were visualized, segmented, and rendered in Horos software (https://horosproject.org).

Specimens examined are housed in the following museum collections: Auckland War Memorial Museum (AIM); Australian Museum, Sydney (AMS); Museum of New Zealand Te Papa Tongarewa (NMNZ); South Australian Museum, Adelaide (SAMA); Western Australian Museum, Perth (WAM); Museum and Art Gallery of the Northern Territory, Darwin (NTM). Institutional abbreviations follow Sabaj (2020). Georeferenced locations for the type specimens of *C. tupareomanaia*, new genus and species, were captured on GPS units and use WGS84 datum.

**Molecular analyses.**—DNA extraction, primers, PCR conditions, sequence alignment, and analysis of COX1 and nuclear sequence data generated for this study, as well as previously published mitochondrial and nuclear sequence data, were performed following protocols described in Hamilton et al. (2017). COX1 sequence data for *C. tupareomanaia*, new genus and species, in this study followed protocols described in Eme et al. (2020). A partial segment of mitochondrial cytochrome c oxidase subunit I (COX1) DNA was sequenced from a tail clipping of a specimen from the type locality of *C. tupareomanaia*, new genus and species, (AIM MA122275) and a specimen of *I. australis* (SAMA F2657). COX1 sequence data was compared to the previously sequenced pygmy pipehorse species *A. breviperula*, *A. tentaculata*, and *I. lummitzeri* (available from Hamilton et al., 2017) in order to calculate genetic distances (uncorrected p-distances) in MEGA v. 7.0.26 (Kumar et al., 2018). The phylogenetic position of the new species was investigated.
among the morphologically similar pygmy pipehorse species *A. breviperula*, *A. tentaculata*, and *I. lumnitzeri*, and sampled members of *Hippocampus* based on the nuclear markers 18s ribosomal (18s) and anonymous putative titin-like protein (TMO-4C4), which were derived in this study and from Hamilton et al. (2017) employing Maximum Likelihood (ML), Maximum Parsimony (MP), and MrBayes analyses (Appendix 1). DNA sequences for the two gene markers were assembled, aligned, and concatenated using Geneious v. 11.1.4 (Biomatters, Ltd., Auckland). The aligned dataset was imported into MEGA v.7.0.26 (Kumar et al., 2018) for ML and MP analyses. ML analyses were evaluated using bootstrapping with 1,000 replicates for topological support. The resulting best scoring ML phylogram was rooted with the southern Australian trunk-brooder pipefish *Heraldia nocturna* and viewed using FIGTREE v.1.3.1 (http://tree.bio.ed.ac.uk/software/figtree/). MP analyses were conducted with 1,000 bootstrap replicates using a full heuristic search utilizing tree-bisection and reconnection (TBR) branch swapping. All characters were weighted equally and unordered. Resulting equally parsimonious cladograms were rooted with *H. nocturna*, summarized using a strict consensus method, and viewed using FIGTREE v.1.3.1. The Bayesian analyses were performed following protocols described in Hamilton et al. (2017) using MrBayes v.3.2 (Ronquist et al., 2012) with settings as follows: GTR substitution model for 18s and TMO-4C4 with a gamma-distributed rate parameter applied, two Metropolis-coupled Markov Chain Monte Carlo (MCMC) runs, and each with four chains. The analyses ran for 10 million generations sampling trees and parameters every 1,000 generations.

**Cylix, new genus**

urn:lsid:zoobank.org:act:B9144B5E-2220-4C29-ABEA-D7CCD4288258

**Type species.**—*Cylix tupareomanaia*, new species.

**Diagnosis.**—A genus of the Syngnathidae that shares numerous morphological synapomorphies with *Acentronura* and *Idiotropiscis*, including head angled ventrally approximately 25° from the principal body axis, enclosed brood pouch, brood pouch plates, prehensile tail, and absence of caudal fin. However, *Cylix tupareomanaia*, new species, differs from all other genera by unique anatomical features of the head, including: a distinct, cup-like crest present anterodorsally on the supraoccipital; and large and conspicuous medioventral conical spines on the cleithral symphysis and the first trunk ring between the pectoral-fin bases. It differs further in having the following combination of morphological characters: prominent supraoccipital; continuous cleithrum; prominent supraclithrum; anterior nuchal plate absent; posterior nuchal plate present with bony dorsomedial crest; large gap present between the supraoccipital and posterior nuchal plate; one to three dorsal spines at midline of snout, posteriormost of these spines large; one large double and rugose lateral head spine present below the cup-like supraoccipital crest; three small blunt lateral head spines on operculum; rim of orbit elevated dorsolaterally and strongly ventrally; two spines on cleithral ring; large rugose spine anterior to ventral third of pectoral-fin base; moderate-sized spine at ventral extent of head; small spine present posterolateral to the pelvic-fin base; four subdorsal spines, forming a square, the dorsal two enlarged.

**Etymology.**—The generic name *Cylix* is derived from the Greek κυλις, meaning cup or chalice, in reference to the cup-like crest present on the head. Gender masculine.

**Cylix tupareomanaia Short, Trnski, and Ngātiwai, new species**

urn:lsid:zoobank.org:act:4DAADA17-DC8E-43EB-81B8-6495E886C05

Common Names: Māori—Tu pare o manaia, English—Manaia

Pygmy Pipehorse

Figures 1–5, Tables 1–5

**Hippocampus jugumus** Kuitter, 2009: 93, figs. A, B (Poor Knights Islands, New Zealand).

**Acentronura australis** Stewart, 2015: 1053, fig. 148.1 (Bay of Islands, New Zealand).

**Idiotropiscis aotearoa** Perkins, 2017 (Whangaruru, New Zealand; http://www.inspiredtodive.com/photo-blog/introducing-idiotropiscis-aotearoa).

**Holotype.**—AIM MA122274, 31.4 mm SL, female, New Zealand, Waiaatapaua Bay, Whangaruru, 35°19′18.7″S, 174°22′08.1″E, depth 14 m, hand collected via SCUBA on vertical rock wall covered in encrusting coralline algae, bryozoans, sponges, solitary corals, turf algae, with *Ecklonia* in adjacent area, C. Bedford, S. Hannam, I. Middleton, G. Short, and T. Trnski, 11 April 2017.

**Paratypes.**—NMNZ P.046322, 55.5 mm SL, male, New Zealand, Bay of Islands, east of Ottorui Rock, 35°14′53.9″S, 174°09′35.1″E, depth 12–17 m, beam trawl, trip code kah0907, RV Kaharoa, shallow rocky reef and soft sediments with a mixture of *Caulerpa*, *Ecklonia*, and red and brown algae, M. Morrison, N. Bagley, NIWA, 3 September 2009; NMNZ P.056154, 35.5 mm SL, female, New Zealand, Cavalli Islands, Cavalli Passage, 35°00′50.4″S, 173°55′26.4″E, depth 12.6–14.5 m, beam trawl, mixture of brown algae, *Ecklonia*, *Caulerpa*, *Lissocoma*, rhodoliths, and assorted red and brown algae, C. and I. Middleton, NIWA, 21 April 2014.

**Diagnosis.**—See generic diagnosis.

**Description.**—Morphometric and meristic characters of the three type specimens listed in Table 1. Trunk rings 13–14; tail rings 35–36; anal-fin rays 4; subdorsal rings 3 (spans one trunk ring and two tail rings); dorsal-fin rays 14; anal-fin rays 4; pectoral-fin rays 14. Body slender; head large relative to body, angled ventrally approximately 25° from the principal body axis, the dorsal profile pyramidal in lateral aspect, rising steeply from snout to elevated and prominent supraoccipital; distinct cup-like crest (SC) present anterodorsally on the head, eye high, moderate, pentameric in dorsal view, divided transversally into two concave sections (Figs. 3, 4); cleithral and supraclithral ridge prominent (Fig. 4); posterior margins of pentameric crest on supraoccipital fused and equal in height to cleithrum; anterior nuchal plate absent; posterior nuchal plate present with bony dorsomedial crest; large gap between the supraoccipital and posterior nuchal plate; Gill openings small, bivalve; rim of orbit with prominent dorsolateral and ventral ridges, fluted with rugose sculpturing; opercular ridge...
low, entire, angled dorsally toward gill opening; swelling of gular region posteroventrally of eye, forming a transverse pair of blunt protuberances; pectoral-fin base without distinct ridges, one strongly elevated ventrolateral bulge (Fig. 4); dorsal-fin origin on 12th trunk ring, fin base elevated; superior trunk ridge discontinuous with superior tail ridge below dorsal-fin base; lateral trunk ridge continuous with inferior tail ridge; inferior tail ridge ends on anal trunk ring; dorsal of anteriormost two trunk rings distinctly broader than posterior trunk rings; trunk in lateral view narrowest at 1st and 2nd trunk rings where angle of head forms from body axis, broadest at 5th trunk ring; principal body ridges distinct and moderately elevated; tail rings of uniform depth over most of length, becoming progressively shorter and smaller near posterior tip; tail prehensile; scutella not evident.

Large spine present on dorsal midline of snout on the ethmoid area, at confluence with the anterior ends of supraorbital ridges, its height extended well above level of nares; none to two smaller medial spines anterior to the large spine on the snout, on the mesethmoid bone (principal dorsal spine and one anterior spine in paratype NMNZ P.056154, principal spine with anterior dorsal spines or elevations absent in paratype NMNZ P.046322); distinct median frontal spine at convergence of anterior edges of the cup-like supraoccipital crest, protruding anteriorly; four lateral head spines, one large double and rugose lateral head spine directly below the cup-like supraoccipital crest, three small blunt spines on operculum aligned 55–58° relative to the ventral axis of the head, the dorsal and ventral blunt spines connecting to terminal elements of the opercular ridge; large, conspicuous midventral conical spines on the cleithral synphys and the first trunk ring between the pectoral-fin bases (Figs. 3, 5); two spines on cleithral ring, large rugose spine anterior to ventral third of pectoral-fin

Fig. 1. *Cylix tupareomanaia*. (A) AIM MA122274, female, holotype shortly after death, 31.4 mm SL; Waiaiapua Bay, Whangaruru, Northland, New Zealand (photograph © Auckland Museum). (B) NMNZ P.056154, female, paratype, shortly after death, 35.5 mm SL; Cavalli Islands, Northland, New Zealand (photograph © Irene Middleton).
base, moderate-sized spine at ventral extent of head; small spine present posterolaterally of the pectoral-fin base (Figs. 3, 5); superior trunk ridges with spines of small to moderate size, enlarged blunt spines dorsally on 3\textsuperscript{rd}, 6\textsuperscript{th}, 10\textsuperscript{th}, 11\textsuperscript{th}, and 12\textsuperscript{th} rings, all bearing dermal flaps; lateral trunk ridges with moderate-sized spines on each trunk ring starting at 2\textsuperscript{nd} ring with enlarged spines on 3\textsuperscript{rd}, 6\textsuperscript{th}, and 10\textsuperscript{th} rings; inferior trunk ridges with moderate-sized spines starting at 3\textsuperscript{rd} ring with enlarged spines on 3\textsuperscript{rd}, 6\textsuperscript{th}, and 10\textsuperscript{th} rings; subdorsal spines four, superior trunk ridge ending with two subdorsal spines,
the anteriormost spine large and conspicuous, superior tail ridge commencing with two subdorsal spines, posteriormost spine reduced, in alignment with larger subdorsal spines above; superior tail ridge spines well developed anteriorly, except on first and second ring, with enlarged spines on 3rd, 4th, 7th, and 11th tail ridges, gradually reducing in size to 22nd trunk ring; lateral tail ridge spines absent; inferior tail ridge spines well developed to 8th tail ring. Simple and branched dermal appendages present on head: long simple appendages extending anteriorly from dorsal rim of orbit, long and branched appendages ventrodorsally of each eye.

*Cylix tupareomanaia* exhibits strong sexual dimorphism with an enclosed brood pouch in male paratype NMNZ P.046322 (Fig. 2). The brood pouch is located along the ventral midline of the tail below the anteriormost ten tail rings. It is enclosed by ten arcuate bony extensions (Fig. 4) that extend ventrolaterally from the anterior ventral plate ridges of the tail, and progressively reduce in size posteriorly. The ten brood pouch plates are similar in appearance, whereas the posteriormost pouch plate is diminutive in size.

**Coloration.**—Holotype in life (Fig. 6A), head, trunk, and tail red; ventrolateral margin of trunk pale red to white; dorsum of head and snout speckled with fine white dots; pentamerous crest on supraoccipital red; snout spines, supraoccipital spine, anterior continuations of supraorbital ridges, and dorsal rim of orbit pale brown to white; white band extending from just behind the eye, grading posteriorly into a reticulated pattern of irregular, roundish quadrilaterals delineated by white coloration, concentrated on operculum and pectoral-fin base; reticulated pattern diffused laterally on head, pale brown to white; dorsal-fin base white with reticulated pattern, proximal third of dorsal-fin red; two parallel rows of rounded quadrilaterals present on trunk and tail rings, four quadrilaterals per ring; medioventral conical spines on the cleithral symphysis and the first trunk ring between the pectoral-fin bases pale brown to white. Fleshy appendages, pale brown to white, present on the frontal spine, principal snout spine, dorsum of rim of orbit, ventrolateral of snout, 3rd and 6th superior trunk ridge spines, and 3rd and 7th superior tail ridge spines. Other individuals of *C. tupareomanaia* observed at the type location and the Poor Knights Islands exhibited red and white countershading coloration or background color typically uniformly pale orange to dark red, respectively (Fig. 6B–F). In alcohol, head and body color pale cream to light brown. Fins hyaline.

**Distribution and habitat.**—*Cylix tupareomanaia* is thus far known only from Taitokerau Northland, New Zealand, including Pāwhairangi (Bay of Islands), Nukutaunga (Cavalli Islands), Tawhiti Rahi and Aorangi (Poor Knights Islands), and the coastal headlands off Whangaruru (Fig. 7). At the type locality, *C. tupareomanaia* was observed in mixed habitat on a vertical rock wall that was covered in encrusting coralline algae, bryozoans, sponges, solitary corals, and turf algae, and which faced a rocky outcrop exposed to the open ocean. The rock wall was subject to moderate ocean swell as was evident from the accumulated debris of detached and decomposed algae on the sandy to rubble bottom of the channel at a depth of 17–18 m. The holotype was collected below the *Ecklonia radiata* kelp line; it was observed moving about in close proximity to another individual of the same
species, which appeared to represent a male–female pair. Additional reef fishes observed on and at the base of the rock wall included: *Gobiopsis atrata* (Gobiidae); *Forsterygion flavonigrum*, *F. maryannae*, and *Notoclinops segmentatus* (Tripterygiidae); *Aplodactylus arctidens* (Aplodactylidae); *Coris sandeyeri* and *Notolabrus tetricus* (Labridae); *Chromis dispilus* (Pomacentridae); and *Chrysophrys auratus* (Sparidae).

Species composition and biodiversity around the North Island of New Zealand indicate subdivision of inshore marine reef ichthyofauna into three regional biogeographic groups or eco-regions, including: western North Island coast; north-eastern North Island coast and offshore islands; and Manawatū Three Kings Islands (Brook, 2002). *Cylix tupareomanaia* may be restricted to the warm temperate waters off the north-eastern coast of the North Island and its offshore islands where it has been collected and observed. The coastal headlands and offshore islands are strongly influenced by oceanic water masses and reflect higher overall species diversity (Brook, 2002); therefore, the new taxon may not occur in the other cooler regional biogeographic areas. Its occurrence further north and south, however, may be confirmed by comprehensive sampling for this cryptic species. The new species is likely endemic to temperate New Zealand; no observations as of yet have been recorded at Rangitāhua the Kermadec Islands, where more than 90% of the coastal ichthyofauna are of subtropical and tropical Indo-Pacific origin, in temperate or tropical Australia, including its offshore subtropical territories of Lord Howe and Norfolk Islands, nor in New Caledonia (Allen et al., 1976; Francis, 1993; Francis and Randall, 1993; Johnson, 1999; Hutchins, 2001; Gomon, 2007; Fricke et al., 2011; Larson et al., 2013; Francis and Duffy, 2015; Trnski et al., 2015; Clark et al., 2017).

![Fig. 4.](image-url)
Cryptic fish assemblages on temperate rocky reefs in New Zealand are dominated by the highly diverse triplefins (Tripterygiidae) and clingfishes (Gobiesocidae) and exhibit a high degree of endemism (Paulin and Roberts, 1993; Hickey et al., 2009; Roberts et al., 2015; Conway et al., 2017, 2018). Other diminutive cryptic reef species recorded include the blennies (Blenniidae), kelpfishes (Clinidae), gobies (Gobiidae), and pipefishes and seahorses (Syngnathidae). The recent discovery of the highly cryptic C. tupareomanaia is therefore a noteworthy addition to reef fish diversity in New Zealand based on the fact it hadn’t been collected or observed in numerous biodiversity surveys of temperate marine ichthyofauna previously conducted in a wide range of habitats. These surveys were carried out in estuaries, shallow coastal bays, seagrass meadows, mangrove forests, open mainland coasts, peninsulas, nearshore islands, and passages within the Bay of Islands (Nicholson, 1979; Nicholson and Roberts, 1980; Francis et al., 2005, 2011; Kelly, 2007; Jones et al., 2009; Gordon et al., 2010), throughout northern New Zealand (Willan et al., 1979; Brook, 2002; Morrison et al., 2002, 2014; Francis et al., 2005; Leathwick et al., 2006; Edgar et al., 2013), along the coast of the East Cape Region (Roberts and Stewart, 2006), at various inshore and offshore islands, including Manawatūhi Three Kings Islands (Hardy et al., 1987), Cavalli Islands (Nicholson, 1979), the Poor Knights Islands (Russell, 1970; Kelly, 2007), Aotea Great Barrier Island (Roberts et al., 1986; Sivaguru and Grace, 2004), the Mokohinau Islands (Housley, 1980), Hen Island (Willis, 1995), Cuvier Islands (Housley et al., 1981), Ahuahu Grea Mercury Island (Grace, 1976), Aldermen Islands (Grace, 1973), the Chatham Islands (Roberts, 1991), in the South Island (Francis, 1979; Leathwick et al., 2006; Gordon et al., 2010; Francis et al., 2011; Morrison et al., 2014), and the sub-Antarctic Auckland Islands (Kingsford et al., 1989).

Cylix tupareomanaia is currently known from very few collected specimens and observations, which suggests that this species occurs in low abundance throughout its range, is hard to find due to its diminutive size and excellent crypsis, only occasionally occurs within SCUBA depths, or is simply rare in the regions where surveys have been conducted. These inferences are supported by the fact that representa-

**Table 1.** Counts and proportional measurements of type specimens of *Cylix tupareomanaia*. Ratios are separated by a colon and are listed as percent of SL, HL, or SnL. Abbreviations: CH (coronet height), DL (dorsal-fin length), HD (head depth), HL (head length), OD (orbital height), PL (pectoral-fin length), PO (post-orbital length), SL (standard length), SnD (snout depth), SnL (snout length), TaL (tail length), TD4 (trunk depth between the 4th and 5th trunk rings), TD9 (trunk depth between the 9th and 10th trunk rings), TrL (trunk length).

| Voucher number | Type | SL (mm) | Trunk rings | Tail rings | Subdorsal trunk rings | Dorsal-fin rays | Anal-fin rays | Pectoral-fin rays | HL:SL | TrL:SL | DL:SL | PL:SL | TaL:SL | TD4:SL | TD9:SL | SnD:SnL | HD:HL | SnL:HL | OD:HL | PO:HL | CH:HL | HL:TrL |
|---------------|------|---------|-------------|------------|----------------------|----------------|--------------|-----------------|-------|-------|-------|-------|--------|--------|--------|--------|------|-------|-------|-------|-------|--------|
| AIM MA122274  | Holotype | 31.4   | 13          | 36         | 3                    | 14             | 4            | 14              | 19.6  | 28.4  | 5.3   | 3.12  | 52.2   | 7.7    | 6.8    | 52.5   | 59.3  | 32.6  | 16.3  | 42.7  | 48.2   | 69.2   |
| NMNZ P.046322 | Paratype | 60.6   | 13          | 35         | 3                    | 14             | 4            | 14              | 14.9  | 26.6  | 5.8   | 3.0   | 58.6   | 8.9    | 6.9    | 55.7   | 67.7  | 42.1  | 15.7  | 40.0  | 52.6   | 55.8   |
| NMNZ P.056154 | Paratype | 39.9   | 14          | 36         | 3                    | 14             | 4            | 14              | 15.6  | 30.8  | 5.76  | 3.1   | 53.6   | 7.30   | 6.9    | 40.2   | 60.8  | 39.2  | 19.4  | 43.5  | 52.2   | 50.6   |
### Table 2.
Morphological counts and proportional measurements for type specimens of *Cylix tupareomanaia* and members of *Acentronura* and *Idiotropiscis*. Measurements are in percent SL and HL. Abbreviations: CH (coronet height), H (holotype), HD (head depth), HL (head length), NT (non-type), P (paratype), PO (post-orbital length), SL (standard length), SnD (snout depth), SnL (snout length), TAL (tail length), TD4 (trunk depth between the 4\textsuperscript{th} and 5\textsuperscript{th} trunk rings), TD9 (trunk depth between the 9\textsuperscript{th} and 10\textsuperscript{th} trunk rings), TrL (trunk length). Lines present, from top to bottom, numbers for standard length (SL), counts for trunk rings, tail rings, dorsal and pectoral fins, and proportions.

| Species                  | *C. tupareomanaia*, new species | *I. australis* | *I. larsonae* | *I. lumnitzeri* | *A. breviperula* | *A. gracilissima* | *A. tentaculata* |
|--------------------------|---------------------------------|---------------|--------------|----------------|----------------|-----------------|-----------------|
| Voucher                  | AIM MA122274                    | NMNZ P.046322 | NMNZ P.056154 | WAM P.33543001 | SAM A.10805-001 | GCRL 21518      | CAS HH-0423     | AM S.105395-001 |
| Type                     | H                               | P             | P            | NT             | NT             | H               | P               | NT              |
| SL (mm)                  | 31.4                            | 60.6          | 39.9         | 54.7           | 50.9           | 33.5            | 33.0            | 69.9            |
| Trunk rings              | 13                              | 13            | 14           | 13             | 13             | 11              | 11              | 11              |
| Tail rings               | 36                              | 35            | 36           | 37             | 37             | 39              | 40              | 45              |
| Subdorsal trunk rings    | 3                               | 3             | 3            | 4              | 4              | 4               | 4               | 4               |
| Dorsal-fin rays          | 14                              | 14            | 14           | 16             | 16             | 17              | 15              | 15              |
| Pectoral-fin rays        | 14                              | 14            | 14           | 15             | 15             | 16              | 15              | 15              |
| HL:SL                    | 16.5                            | 14.7          | 15.6         | 15.1           | 15.1           | 15.3            | 14.4            | 14.2            |
| TrL:SL                   | 28.3                            | 26.6          | 30.8         | 24.3           | 26.3           | 24.8            | 26.2            | 18.6            |
| TD:SL                    | 54.2                            | 58.6          | 53.6         | 60.5           | 61.7           | 62.7            | 52.5            | 67.2            |
| TD9:SL                   | 6.8                             | 6.9           | 9.6          | 9.3            | 9.3            | 14.6            | 10.9            | 6.9             |
| SnD:SnL                  | 52.5                            | 55.7          | 40.2         | 46.2           | 37.6           | 60.4            | 75.4            | 54.7            |
| HD:HL                    | 59.3                            | 67.7          | 60.8         | 59.0           | 50.9           | 72.0            | 73.0            | 60.4            |
| SnL:HL                   | 32.6                            | 42.1          | 39.2         | 31.9           | 38.3           | 29.0            | 24.9            | 33.1            |
| PO:HL                    | 42.7                            | 40.6          | 43.5         | 48.0           | 47.4           | 46.1            | 51.3            | 52.3            |
| CH:HL                    | 48.2                            | 52.6          | 52.2         | 34.5           | 43.9           | 66.1            | 67.7            | 39.4            |
| HL:TrL                   | 63.1                            | 55.8          | 50.7         | 62.2           | 57.6           | 61.9            | 54.9            | 76.6            |

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tives of *Idiotropiscis* in southern Australia are uncommon in its respective distributions; only two records currently exist for *I. larsonae*, and seven for *I. australe* (OZCAM museum record search; https://ozcam.ala.org.au/occurrences/search?taxa=Idiotropiscis#tab_recordsView).

**Etymology.**—The species epithet *tupareomanaia* is a neologism gifted by kaumātua (tribal elders) of Ngātiwai and references Home Point adjacent to the type locality, referred to by Ngātiwai as Tu Pare o Huia, meaning “the plume of the huia”; the huia was a bird that became extinct in the early 20th century. Tu Pare o Manaia translates as “the garland of the Manaia.” The pare, or garland, references the pentamerous head crest of the new species, and Manaia is the Māori name for a seahorse, and is also an ancestor that appears as a stylized figure used in Māori carvings representing a guardian.

**Remarks.**—Apparent ontogenetic differences in morphological features of the head were observed between the specimens of *C. tupareomanaia* examined herein (Fig. 2). The smallest female (Fig. 2A, AIM MA122274, 31.4 mm SL, holotype) exhibits a cup-like crest on the supraoccipital that is highly elevated anteriorly, distinct median supraoccipital spine at convergence of anterior edges of the coronet, protruding well anteriorly; three dorsal spines at midline of snout on mesethmoid bones, exceptionally large principal dorsal spine at confluence with anterior continuations of supraorbital ridges, the two anterior dorsal spines small, and the lateral head spine directly ventral of the cup-like supraoccipital crest consists of distinct but small paired spines. The morphological features in the larger female paratype (Fig. 2B, NMNZ P.056154, 35.5 mm SL) are less pronounced: the median supraoccipital spine presents as a distinct but blunt spine protruding anteriorly, the snout spines, and the lateral head spine directly ventral of the cup-like supraoccipital crest consists of distinct but small paired spines.

### Table 3. Comparison of meristic and morphometric characters between *Cylix tupareomanaia* and members of *Acentronura* and *Idiotropiscis*. Abbreviations: HT (Holotype), NT (Non-type), PT (Paratype).

| Species          | *C. tupareomanaia*, new species | *I. australe* |
|------------------|--------------------------------|--------------|
| Type             | HT                             | NT           |
| Voucher number   | AIM MA122274                  | P.046322     |
| Trunk rings      | 13                             | 13           |
| Tail rings       | 36                             | 35           |
| Subdorsal trunk rings | 3                        | 3            |
| Dorsal-fin rays  | 14                             | 13           |
| Pectoral-fin rays | 14                            | 14           |
| Superior and inferior trunk and tail ridges | Discontinuous | Discontinuous |
| Cup-like crest on supraoccapital | Present | Present |
| Dorsomedial bony crest on supraoccapital | Absent | Absent |
| Dorsomedial bony crest on first trunk ring | Present | Present |
| Bilateral protuberances present lateroposteriorly on posttemporal | Absent | Absent |
| Large rugose lateral head spine | Present | Present |
| 3 small lateral head spines | Present | Present |
| Frontal spine    | Present                        | Present      |
| Snout spines     | Present                        | Present      |
| Midventral conical spines on cleithral symphysis and first trunk ring | Present | Present |
| Cleithral ring confluent | Present | Present |
| Cleithral ring spine on pectoral-fin base | Present | Present |
| Cleithral ring spine ventrally of first trunk ring | Present | Present |
| Small spine ventroposteriorly of pectoral-fin base | Present | Present |
| Subdorsal spines | Present                        | Present      |
| Orbital rim extension | Present | Present |
| Swelling of gular region ventroposterior to eye | Present | Present |
| Superior trunk ridge spines | 3, 6, 10 | Absent |
| Superior tail ridge spines | 4, 7, 11 | Absent |
| Anal-fin         | Present                        | Present      |

### Table 4. Summary of the number of trunk rings spanning the brood pouch in male specimens of *C. tupareomanaia* and members of *Acentronura* and *Idiotropiscis*.

| Species          | *C. tupareomanaia* | *A. breviperula* | *A. gracilissima* | *A. tentaculata* | *I. australe* | *I. larsonae* | *I. lumnitzeri* |
|------------------|--------------------|------------------|-------------------|------------------|---------------|---------------|----------------|
| Voucher          | NMNZ P.046322      | BMNH 1890.1.14.51| CAS-SU 6681       | BMNH 1869.6.21.7| WAM P.33543.001| NTM S.10805-001| AMS I38660-001|
| Type             | Paratype           | Holotype         | Non-type          | Holotype         | Non-type      | Non-type      | Holotype       |
| Trunk rings      | 8                  | 7                | 14                | 12               | 10            | 8             | 11             |
possesses two dorsal spines, the principal spine and one small anterior spine, and the lateral head spine directly ventral of the bony pentamerous bony crest consists of small but merged paired spines. In contrast, the adult male paratype (Fig. 2C, NMNZ P.046322, 55.5 mm SL) exhibits a cup-like supraoccipital crest that is low, less elevated, angled somewhat posteriorly, and cup-like in dorsal view, the median frontal spine a minute but discernible ridge, wedge-like in appearance, one large principal spine at midline of snout, and the lateral head spine directly ventral of the pentamerous bony crest is merged as one rugose spine.

**Acentronura Kaup, 1853**

**Diagnosis.**—A genus of the Syngnathidae that shares numerous morphological synapomorphies with *Cylix* and *Idiotropiscis*, including head angled ventrally approximately 25° from the principal body axis, enclosed brood pouch, brood

**Table 3.** Morphological character comparisons between *Hippocampus* and the pygmy pipehorse genera *Cylix* and *Idiotropiscis*.

| Species                                      | Hippocampus spp. | C. tupareomanaia | I. australis | I. larsonae | I. lumnitzeri |
|----------------------------------------------|------------------|------------------|-------------|-------------|--------------|
| Coronet                                      | Present          | Present          | Absent      | Absent      | Absent       |
| Subdorsal rings 4                           | Present          | Present          | Present     | Absent      | Absent       |
| Parietal spine                              | Present          | Present          | Absent      | Absent      | Absent       |
| Lateral head spines ventral of coronet      | Present          | Present          | Absent      | Absent      | Absent       |
| Snout spine                                 | Present          | Present          | Absent      | Absent      | Absent       |
| Cleithral ring spines                       | Present          | Present          | Absent      | Absent      | Absent       |
| Subdorsal spines                            | Present          | Present          | Absent      | Absent      | Absent       |
| Enlarged superior trunk spines              | Present          | Present          | Absent      | Absent      | Absent       |
| Enlarged superior tail spines               | Present          | Present          | Absent      | Absent      | Absent       |
| Enlarged spines on lateral and inferior trunk spines | Present        | Present          | Absent      | Absent      | Absent       |
| Eye spines                                  | Present          | Absent           | Absent      | Absent      | Absent       |
| Elevated rims of orbit                      | Absent           | Present          | Absent      | Absent      | Absent       |
pouch plates, prehensile tail, and absence of caudal fin. However, *Acentronura* differs from its co-familials by the following combination of characters: supraoccipital low, not elevated, with distinct dorsomedial crest, followed by an elevated bony dimple; bilateral bony lobed protuberances on the posterolateral margins of the post-temporal bones; anterior nuchal plate absent; posterior nuchal plate present anterior to cleithrum with dorsomedial crest-like ridge along its dorsum, large gap present between the supraoccipital and posterior nuchal plate; small blunt spine midway between orbit and lobed protuberance on operculum; cleithral ring distinct, discontinuous mid-dorsally; single gill slit between supraoccipital and cleithral ridge; rim of orbit projecting dorsolaterally and slightly ventrolaterally; spines absent on principal trunk and tail ridges.

Fig. 6. *Cylix tupareomanaia* in situ. (A) AIM MA122274, female, holotype, Waiatapua Bay, Whangaruru, Northland, New Zealand, 12 m depth (photograph © Shane Housham). (B) Waiatapua Bay, Whangaruru, Northland, New Zealand, 12 m depth (photograph © Shane Housham). (C) Waiatapua Bay, Whangaruru, Northland, New Zealand, 12 m depth (photograph © Richard Smith). (D) Waiatapua Bay, Whangaruru, Northland, New Zealand, 12 m depth (photograph © Irene Middleton). (E) Waiatapua Bay, Whangaruru, Northland, New Zealand, 12 m depth (photograph © Irene Middleton). (F) Poor Knights Islands, Northland, New Zealand, at 10 m depth (photograph © Kent Erickson).
Type species.—Hippocampus gracilissimus Temminck and Schlegel, 1850.

Acentronura breviperula Fraser-Brunner and Whitley, 1949
Figures 8A, 9A, 10A, 11A; Tables 2–4

Acentronura breviperula Fraser-Brunner and Whitley, 1949: 148, fig. 1 (Mabuiag, Torres Strait, Queensland).

Diagnosis.—See generic diagnosis. Acentronura breviperula differs from its congeners by the following combination of characters: supraoccipital consisting of a distinct bony bipartite dorsomedial crest, segments arcuate in lateral view, followed by an elevated and long bony dimple; posterior margin of second segment of dorsomedial crest merging within the bony dimple, which is approximately one-third longer than the dorsomedial crest and tapered posteriorly.

Description.—Morphometric and meristic characters listed in Tables 2–4. Superior trunk and tail ridges discontinuous below dorsal-fin base, lateral tail ridge present, inferior trunk ridge ends at anal ring, lateral trunk ridge confluent with inferior tail ridge. Head angled ventrally 25° from the principal body axis, the anterodorsal profile slightly conoid in lateral aspect; supraoccipital low, not elevated, with a distinct bony bipartite dorsomedial crest, segments arcuate in lateral view, followed by an elevated and long bony dimple; posterior margin of second segment of dorsomedial crest merging within the bony dimple, which is approximately one-third longer than the dorsomedial crest and tapered posteriorly.

Distribution.—Acentronura breviperula is known from the tropical Indo-West Pacific, from East Africa, Madagascar, the Red Sea, Persian Gulf, Papua New Guinea, Torres Strait, northern Great Barrier Reef, Australia, New Caledonia, and Taiwan (Fraser-Brunner and Whitley, 1949; Dawson, 1985; Kuiter, 2000, 2003; Fricke and Kulbicki, 2006; Chen, 2017; Fricke et al., 2019).

Material examined.—Acentronura breviperula: CAS 247135, female, 40.1 mm SL, channel between Iles aux Canards and Noumea, Anse Vate Bay, New Caledonia, 22°18’23.8”S, 166°26’07.9”E, depth 23 m, H. Hamilton and G. Short, 18 October 2008.

Acentronura gracilissima Temminck and Schlegel, 1850
Figures 8B, 9B; Tables 2–4

Hippocampus gracilissimus Temminck and Schlegel, 1850: 274, pl. 120, fig. 6 (Japan).

Atelurus germani Duméril, 1870: 584 (Cochin, China).

Diagnosis.—See generic diagnosis. Acentronura gracilissima differs from its congeners by the following combination of characters: supraoccipital consisting of a distinct dorsomedial crest, non-segmented, ridge-like in lateral view, followed by an elevated and bony dimple; bony dimple approximately one-third in length of dorsomedial crest.
Fig. 8. Lateral view of preserved specimens of Acentronura spp. redescribed in this study. (A) *A. breviperula*, CAS 247135, female, 40.1 mm SL. (B) *A. gracilissima*, CAS-SU 6681, male, 70.4 mm SL. (C) *A. tentaculata*, CAS 247139, male, 50.8 mm SL. (D) *A. tentaculata*, CAS 247139, female, 53.9 mm SL.
Description.—Morphometric and meristic characters listed in Tables 2–4. Superior trunk and tail ridges discontinuous below dorsal-fin base, lateral tail ridge present, inferior trunk ridge ends at anal ring, lateral trunk ridge confluent with inferior tail ridge. Head angled ventrally 25° from the principal body axis, the anterodorsal profile slightly conoid in lateral aspect; supraoccipital, low, not elevated, with a distinct dorsomedial crest, non-segmented, ridge-like in lateral view, followed by an elevated and bony dimple; bony dimple approximately one-third in length of dorsomedial...
Fig. 10. Dorsal view of μCT scanned neurocranium of (A) *Acentronura breviperula*, CAS 247135, female; (B) *Acentronura gracilissima*, CAS 247139, male; (C) *Acentronura tentaculata*, CAS-SU 6681, male. Abbreviations: BLP, bilateral lobed protuberances; SC, supraoccipital crest.
Fig. 11. X-ray radiography of (A) *A. breviperula*, BMNH 1890.1.14.51, male, holotype; (B) *A. tentaculata*, BMNH 1869.6.21.7, male, holotype; (C) *I. larsonae*, NTM S.10805-001, male, holotype, 55.5 mm SL (Photograph credits for *A. breviperula* and *A. tentaculata* to Oliver Crimmen and Ralf Britz, © The Trustees of the Natural History Museum, London; *I. larsonae* to Michael Hammer, © Museum and Art Gallery of the Northern Territory).
crest; bilateral bony lobed protuberances on the posterolateral margins of the post-temporal bones (Fig. 10B); anterior nuchal plate absent (Fig. 9B); posterior nuchal plate present anterior to cleithrum with dorsomedial crest-like ridge along its dorsum, large gap present between the supraoccipital and posterior nuchal plate; small blunt spine midway between orbit and lobed protuberance on operculum; cleithral ring distinct, discontinuous mid-dorsally; single gill slit between supraoccipital and cleithral ridge; rim of orbit projecting dorsolaterally and slightly ventrolaterally; snout spine absent; interorbital narrow, depressed; opercular ridge distinct, entire, angled dorsally toward gill opening; swelling of gular region ventroposterior to orbit absent; pectoral-fin base without distinct ridges, low, strongly elevated ventrolateral bulge supporting the pectoral-fin absent; trunk deepest anteriorly, principal body ridges distinct; principal body ridge spines absent; caudal fin absent. *Acentronura gracilissima* exhibits strong sexual dimorphism associated with the presence of a male brood pouch. The brood pouch is formed along the ventral midline of the tail and is present below the anteriormost 14 tail rings (Fig. 8B). \(\mu\)CT scanning of the specimen (Fig. 9B) revealed the brood pouch is enclosed by 14 arcuate bony extensions, which extend ventrolaterally from the anterior ventral plate ridges of the tail and are reduced in size posteriorly. The anteriormost pouch plate is broad and paddle-shaped at ventrocaudal margin and curved posterolaterally relative to other pouch plates. The second pouch plate appears to consist of double arcuate bony extensions merged as one bony extension. The posteriormost pouch plate is diminutive in size.

**Distribution.**—*Acentronura gracilissima* is known from the tropical western Pacific from New Caledonia, Japan, Indonesia, and the South China Sea (Dawson, 1985; Rivaton and Richer de Forges, 1990; Randall and Lim, 2000; Nakae et al., 2018; Araki et al., 2019).

**Material examined.**—*Acentronura gracilissima*: CAS-SU 6681, 70.4 mm SL, Honshu Island, Sagami Sea, Japan, 35°09'34.0"N, 139°29'37.9"E, date collected 1900.

*Acentronura tentaculata* Günther, 1870

Figures 8C–D, 9C–D, 11B; Tables 2–4

*Acentronura tentaculata* Günther, 1870: 516 (Suez, Egypt).

**Syngnathoides algensis** Fournonaro, 1954: 210 (Dzaoudzi, Mayotte Island, Commore Island).

*Acentronura mossambica* Smith, 1963: 522, pl. 76, figs. f, g (Inhaca and Inhambane Estuary, Mozambique).

**Diagnosis.**—See generic diagnosis. *Acentronura tentaculata* differs from its congeners by the following combination of characters: supraopercipital consists of distinct bony bipartite dorsomedial crest, segments arcuate in lateral view, followed by an elevated and bony dimple; posterior margin of second segment of dorsomedial crest located at opening of, but not merged within, the bony dimple, which is approximately equal in length to the dorsomedial crest and tapered posteriorly. Superior trunk and tail ridges discontinuous below dorsal-fin base, lateral tail ridge present, inferior trunk ridge ends at anal ring, lateral trunk ridge confluent with inferior tail ridge. Head angled ventrally 25° from the principal body axis, the anterodorsal profile slightly conoid in lateral aspect; supraopercipital, low, not elevated, with a distinct bony bipartite dorsomedial crest, segments arcuate in lateral view, followed by an elevated and bony dimple; posterior margin of second segment of dorsomedial crest located at opening of, but not merged within, the bony dimple, which is approximately equal in length to the dorsomedial crest and tapered posteriorly; bilateral bony lobed protuberances on the posterolateral margins of the post-temporal bones (Fig. 10C); anterior nuchal plate absent (Fig. 9C–D); posterior nuchal plate present anterior to cleithrum with dorsomedial crest-like ridge along its dorsum, large gap present between the supraopercipital and posterior nuchal plate; small blunt spine midway between orbit and lobed protuberance on operculum; cleithral ring distinct, discontinuous mid-dorsally; single gill slit between supraoccipital and cleithral ridge; rim of orbit projecting dorsolaterally and slightly ventrolaterally; snout spine absent; interorbital narrow, depressed; opercular ridge distinct, entire, angled dorsally toward gill opening; swelling of gular region ventroposterior to orbit absent; pectoral-fin base without distinct ridges, low, strongly elevated ventrolateral bulge supporting the pectoral-fin absent; trunk deepest anteriorly, principal body ridges distinct; principal body ridge spines absent; caudal fin absent. *Acentronura tentaculata* exhibits strong sexual dimorphism associated with the presence of a male brood pouch. The brood pouch is formed along the ventral midline of the tail and is present below the anteriormost 12 tail rings (Fig. 8C–D). \(\mu\)CT scanning of the material (Fig. 9C–D) revealed the brood pouch is enclosed by 12 arcuate bony extensions, which extend ventrolaterally from the anterior ventral plate ridges of the tail and are reduced in size posteriorly. The anteriormost pouch plate is broad and paddle-shaped at ventrocaudal margin and curved posterolaterally relative to other pouch plates. The posteriormost pouch plate is diminutive in size.

**Distribution.**—*Acentronura tentaculata* is known from the tropical Indo-West Pacific, from East Africa, Madagascar, the Red Sea, Arabian and Persian gulfs to Torres Strait, Philippines, the northern Great Barrier Reef, Australia, and New Caledonia (Dawson, 1985; Rivaton and Richer de Forges, 1990; McKenna, 2003; Fricke and Kulbicki, 2006; Al-Jufaili et al., 2010; Grandcourt, 2012; Nakae et al., 2018).

**Material examined.**—*Acentronura tentaculata*: CAS 247139, male, 50.8 mm SL, female, 53.9 mm SL, Tamaraw Beach, South Puerto Galera, Philippines, 13°30'03.8"N, 120°53'40.2"E, Hearst Philippine Biodiversity Expedition, station PG-011, B. Moore and H. Hamilton, 3 June 2011.

*I. tetradactyla* Whitley, 1947

**Diagnosis.**—A genus of the Syngnathidae that shares numerous morphological synapomorphies with *Acentronura* and *Cylix*, including head angled ventrally approximately 25° from the principal body axis, enclosed brood pouch, brood pouch plates, prehensile tail, and absence of caudal fin. However, *Idiotropiscis* differs from its co-familials by the following combination of characters: supraopercipital is elevated with a distinct and raised bony dorsomedial crest; posterolateral margins of post-temporal bones expanded...
moderately anteriorly taking the form of protuberances; anterior nuchal plate absent; posterior nuchal plate present anterior to cleithrum with dorsomedial crest-like ridge along its dorsum, large gap present between the supraoccipital and posterior nuchal plate; small blunt spine midway between orbit and lobed protuberance on operculum; cleithral ring distinct, discontinuous mid-dorsally; bilateral gill slits situated laterally on head between supraoccipital and cleithrum.

**Idiotropiscis australis** (Waite and Hale, 1921)

Figures 12, 13; Tables 2–5

_Acentronura australis_ Waite and Hale, 1921: 317–318, fig. 53 (St. Vincent Gulf, South Australia).

**Diagnosis.**—See generic diagnosis. _Idiotropiscis australis_ differs from its congeners by the following combination of characters: distinct raised bony multipartite dorsomedial crest on the supraoccipital, the four segments arcuate in lateral view, spanning the complete frontal from anterior margins of the interorbital to the supraoccipital, protruding anteriorly; posterolateral margins of post-temporal bones expanded moderately anteriorly taking the form of curved protuberances; small dorsal snout spine present medially on mesethmoid bone.

**Description.**—General body shape as in Figure 13. Morphometric and meristic characters listed in Tables 2–4. Superior trunk and tail ridges discontinuous below dorsal-fin base, lateral tail ridge present, inferior trunk ridge ends at anal ring, lateral trunk ridge confluent with inferior tail ridge. Head angled ventrally 25° from the principal body axis, the anterodorsal profile slightly conoid in lateral aspect, rising from short snout to an elevated supraoccipital; distinct raised bony multipartite dorsomedial crest on the supraoccipital, the four segments arcuate in lateral view, spanning the complete frontal from anterior margins of the interorbital to the supraoccipital, protruding anteriorly; posterolateral margins of post-temporal bones expanded moderately anteriorly taking the form of curved protuberances (Fig. 14A); anterior nuchal plate absent (Fig. 13A); posterior nuchal plate present anterior to cleithrum with dorsomedial crest-like ridge along its dorsum, large gap present between the supraoccipital and posterior nuchal plate; small blunt spine midway between orbit and lobed protuberance on operculum; cleithral ring distinct, discontinuous mid-dorsally; gill openings as small bilateral slits directly situated laterally on head between supraoccipital and cleithrum; small dorsal snout spine present medially on mesethmoid bone; interorbital narrow, depressed; opercular ridge low, entire, angled dorsally toward gill opening; slight swelling of gular region ventroposterior to eye; pectoral-fin base without distinct ridges, on strongly elevated ventrolateral bulge; trunk deepest anteriorly, principal body ridges distinct; principal body ridge spines absent. Caudal fin absent. _Idiotropiscis australis_ exhibits strong sexual dimorphism associated with the presence of a male brood pouch. The brood pouch is formed along the ventral midline of the tail and is present below the anteriormost 11 tail rings (Fig. 12A). µCT scanning of the material (Fig. 13A) revealed the brood pouch is enclosed by 11 arcuate bony extensions, which extend ventrolaterally from the anterior ventral plate ridges of the tail and are reduced in size posteriorly. The anteriormost pouch plate is broad and paddle-shaped at ventrocaudal margin and curved posterolaterally relative to other pouch plates. The posteriormost pouch plate is diminutive in size.

**Distribution.**—_Idiotropiscis australis_ is endemic to the temperate waters of southern and southwestern Australia, from

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**Fig. 12.** Lateral view of preserved specimens of _Idiotropiscis_ spp. redescribed in this study. (A) _I. australis_, WAM P.33543-001, male, 54.7 mm SL. (B) _I. larsonae_, NTM S.10805-001, male, holotype, 33.5 SL. (C) _I. larsonae_, GCRL 21518, female, paratype, 33.0 mm SL. (D) _I. lumnitzeri_, CAS HH-0423, male, 69.9 mm SL. (E) _I. lumnitzeri_, AMS I.45395-001, female, 54.0 mm SL.
Fig. 13. Lateral view of μCT scanned skeletons of preserved specimens of *Idiotropiscis* spp. redescribed in this study. (A) *I. australis*, WAM P.33543-001, male, 54.7 mm SL. (B) *I. larsonae*, GCRL 21518, female, paratype, 33.0 mm SL. (C) *I. lumnitzeri*, CAS HH-0423, male, 69.9 mm SL. (D) *I. lumnitzeri*, AMS I.45395-001, female, 54.0 mm SL.
Fig. 14. Dorsal view of μCT scanned neurocranium of the head of (A) *Idiotropiscis australis*, WAM P.33543-001, male; (B) *Idiotropiscis larsonae*, GCRL 21518, male; (C) *Idiotropiscis lumnitzeri*, CAS HH-0423, male. Abbreviations: BLP, bilateral lobed protuberances; SC, supraoccipital crest.
Cape Jarvis and the Gulf St Vincent, South Australia, and Carnac Island, Western Australia (Dawson, 1985).

**Material examined.**—*Idiotropiscis australis*: SAMA F2657, Yankalilla, South Australia, Australia, 35.597767°S, 138.097511°E, depth 20 m; WAM P.25346-015, Australia, Western Australia, Carnac Island, Gage Roads, dredge, J. Scott, 30 June 1975; WAM P.33542-001, Success Bank, Cockburn Sound, Western Australia, 32.083097°S, 115.683344°E, depth 4 m, 3 November 1997; WAM P.33543-001, male, Owen Anchorage, Cockburn Sound, Western Australia, Australia, 32.114459°S, 115.749989°E, depth 12 m, 1 November 1997.

**Idiotropiscis larsonae** (Dawson, 1984)

Figures 11–13, Tables 2–5

*Acentronura (Idiotropiscis) larsonae* Dawson, 1984: 157–158, figs. 1, 2 (Alpha Island, Monte Bello Islands, Western Australia).

**Diagnosis.**—See generic diagnosis. *Idiotropiscis larsonae* differs from its congeners by the following combination of characters: bony dorsomedial crest on the supraoccipital, strongly elevated, tripartite, the three large segments arcuate in lateral view, spanning the complete frontal from anterior margins of the interorbital to the supraoccipital, compressed laterally, protruding anteriorly; posterolateral margins of post-temporal bones expanded slightly anteriorly taking the form of flat protuberances, not prominent; rim of orbit projecting slightly dorsolaterally and ventrolaterally; small dorsal snout spine present medially on mesethmoid bone; body compressed laterally.

**Description.**—Morphometric and meristic characters listed in Tables 2–4. Superior trunk and tail ridges discontinuous below dorsal-fin base, lateral tail ridge present, inferior trunk ridge ends at anal ring, lateral trunk ridge confluent with inferior tail ridge. Head angled ventrally 25° from the principal body axis, the anterodorsal profile slightly conoid in lateral aspect; bony dorsomedial crest on the supraoccipital, strongly elevated, tripartite, the three large segments arcuate in lateral view, spanning the complete frontal from anterior margins of the interorbital to the supraoccipital, compressed laterally, protruding anteriorly; posterolateral margins of post-temporal bones expanded slightly anteriorly taking the form of flat protuberances, not prominent; rim of orbit projecting slightly dorsolaterally and ventrolaterally; small dorsal snout spine present medially on mesethmoid bone; body compressed laterally.

**Diagnosis.**—See generic diagnosis. *Idiotropiscis larsonae* differs from its congeners by the following combination of characters: bony dorsomedial crest on the supraoccipital, strongly elevated, tripartite, the three large segments arcuate in lateral view, spanning the complete frontal from anterior margins of the interorbital to the supraoccipital, compressed laterally, protruding anteriorly; posterolateral margins of post-temporal bones expanded slightly anteriorly taking the form of flat protuberances, not prominent; rim of orbit projecting dorsolaterally and ventrolaterally; small dorsal snout spine present medially on mesethmoid bone; body compressed laterally.

**Description.**—Morphometric and meristic characters listed in Tables 2–4. Superior trunk and tail ridges discontinuous below dorsal-fin base, lateral tail ridge present, inferior trunk ridge ends at anal ring, lateral trunk ridge confluent with inferior tail ridge. Head large relative to body; angled ventrally 25° from the principal body axis, the anterodorsal profile conoid in lateral aspect; rising steeply from short snout to a prominent supraoccipital; large, prominent, and raised bony dorsomedial crest on the supraoccipital, dome-like in lateral view, protruding anteriorly; posterolateral margins of post-temporal bones expanded moderately anteriorly taking the form of tapered and wing-like protuberances; rim of orbit projecting dorsolaterally and ventrolaterally; one large and blunt spine on cleithral at level of last pectoral-fin ray; small spine posterolateral to pectoral fin; superior trunk ridge with enlarged spines projecting dorsolaterally on 6th and 10th trunk rings; subdorsal spines four, last two superior trunk ridges ending under dorsal fin with subdorsal spines, first two superior tail ridges under dorsal fin with subdorsal spines.

**Description.**—Morphometric and meristic characters listed in Tables 2–4. Superior trunk and tail ridges discontinuous below dorsal-fin base, lateral tail ridge present, inferior trunk ridge ends at anal ring, lateral trunk ridge confluent with inferior tail ridge. Head large relative to body; angled ventrally 25° from the principal body axis, the anterodorsal profile conoid in lateral aspect; rising steeply from short snout to a prominent supraoccipital; large, prominent, and raised bony dorsomedial crest on the supraoccipital, dome-like in lateral view, dorsocaudal margin irregular, protruding anteriorly; posterolateral margins of post-temporal bones expanded moderately anteriorly taking the form of tapered and wing-like protuberances (Fig. 14C); cleithral ring distinct, prominent, discontinuous mid-dorsally; anterior nuchal...
plate absent; posterior nuchal plate present anterior to cleithrum with dorsomedial crest-like ridge along its dorsum, large gap present between the supraoccipital and posterior nuchal plate; cleithral ring distinct, low, discontinuous mid-dorsally at bony dorsomedial crest; rim of orbit projecting dorsolaterally; opercular ridge low, entire, angled dorsally toward gill opening; swelling of gular region ventroposterior to eye forming a transverse pair of blunt protuberances; pectoral-fin base without distinct ridges, on strongly elevated ventrolateral bulge (Fig. 15); trunk narrowest at 3rd and 4th ring; dorsum of 2nd, 3rd, and 4th trunk rings noticeably broader than 5–11th trunk rings; dorsal-fin base strongly raised dorsally; subdorsal rings four (spans two and a half trunk rings and one and a half tail rings), dorsal-fin base starting immediately posterior to 10th trunk ring and ending immediately posterior to 2nd tail ring; caudal fin absent. Body simple and branched dermal flaps present on anterior part of under dorsal fin with subdorsal spines, first two superior tail spines projecting dorsolaterally on 6th and 10th trunk rings; subdorsal spines four, last two superior trunk rings ending under dorsal fin with subdorsal spines, first two superior tail ridges under dorsal fin with subdorsal spines (Fig. 15B); large simple and branched dermal flaps present on anterior part of frontal ridge, ventral to eye, 4th and 7th superior trunk ridges, 7–9th lateral and inferior trunk ridges, and on 5th, 10th, 15th, 19th, and 24th superior and inferior tail ridges. The female specimen (AMS 1.45395-001) exhibits well-developed ossification of the inferior and ventral trunk area as detected by μCT scanning (Fig. 13D). Idiotropiscis lumnitzeri exhibits strong sexual dimorphism associated with the presence of a male brood pouch. The brood pouch is formed along the ventral midline of the tail and is present below the anteriormost 11 tail rings (Fig. 12D). μCT scans revealed the brood pouch is enclosed by 11 arcuate bony extensions (Figs. 13C, 15B), which extend ventrolaterally from the anterior ventral plate ridges of the tail, are reduced in size posteriorly, the anteriormost extension and curved posterolaterally relative to the other extensions.

**Distribution.**—Idiotropiscis lumnitzeri is endemic to the temperate waters of southeastern Australia, from Cabbage Tree Bay, Manly, to Brush Island located south of Ulladulla Harbour, New South Wales (Kuiter, 2004).

**Material examined.**—Idiotropiscis lumnitzeri: AMS 1.45395-001, female, 54.0 mm SL, N of Burrewarra Point, S of Batemans Bay, New South Wales, Australia, depth 22 m; CAS HH-0423, male, 69.9 mm SL, SW of Bare Island, Botany Bay, NSW, Australia, 33°59′33.3″S, 151°13′47.3″E, depth 18 m, 1 March 2007.

**DISCUSSION**

All previous descriptions of pygmy pipehorses are based only on one or two specimens in which the internal (skeletal) anatomy of the described species was undocumented. (e.g., Temminck and Schlegel, 1850; Günther, 1870; Waite and Hale, 1921; Fraser-Brunner and Whitley, 1949; Dawson, 1984; Kuiter, 2004). Our description of C. tupareomanaia is also derived from a small number of individuals (holotype and two paratypes), but contrary to these previous descriptions, we have observed elements in the skeleton of C. tupareomanaia using micro-computed tomography from which we have identified key diagnostic features, especially of the neurocranium (see diagnosis). The morphological details would have been impossible to obtain from traditional radiographs alone.

**Comparative morphological studies among pygmy pipe-horses.**—Cylix tupareomanaia and members of Acentronura and Idiotropiscis (Figs. 10–17), despite being superficially similar in outward appearance, exhibit significant morphological differences among them in the neurocranium that aid in their diagnoses. The main neurocranial distinctions were observed in the morphology of the supraoccipital crests and bilateral bony lobed protuberances on the posterolateral margins of the post-temporal bones. The characters that distinguish Cylix tupareomanaia from the members of Idiotropiscis are presented in Tables 2–5 and summarized below. Cylix tupareomanaia is unique in Syngnathidae in possessing a highly derived bony cup-like crest present anterodorsally on the supraoccipital and large, conspicuous conical spines ventrally centered on the head on the cleithral symphysis and the first trunk ring between the pectoral-fin bases, which we propose as apomorphies for this species. Cylix tupareomanaia is most similar to members of Idiotropiscis (Tables 2–4) in meristic and morphometric characters and in the following morphological and neurocranial characters: principal ridge configuration; elevated supraoccipital; absence of anterior nuchal plate presence of posterior nuchal plate, with large gap between it and the supraoccipital; presence of a bony dorsomedial crest on the dorsum of the posterior nuchal plate; pronounced ventrolateral bulge supporting the pectoral-fin base; and certain body spines (snout spines in I. australae and I. larsonae; four subdorsal spines, large cleithral ring spine at level of last pectoral-fin ray, and small spine present posterolateral to the pelvic fin in I. lumnitzeri [Fig. 14]).

Cylix tupareomanaia differs primarily from the members of Idiotropiscis by features of the crest morphology on the supraoccipital bone (cup-like pentameric crest [Figs. 1–4] vs. the presence of a thin bony dorsomedial crest [Figs. 12–15]) and large midventral spines on the cleithral symphysis and the first trunk ring between the pectoral-fin bases (Figs. 4–6; vs. absence of midventral spines and presence of flat surface venter of head and first trunk ring [Figs. 12–13, 15]). Additional distinguishing characters include the absence of bilateral bony lobed protuberances on the posterolateral margins of the post-temporal bones (vs. presence in all members of Acentronura and Idiotropiscis [Figs. 12, 16]), the presence of the supraclithrum that extends dorsally from the cleithrum, forming a continuous bony collar (Fig. 5) vs. absence of a supraclithrum resulting in cleithra terminating at the anterior margins of the bony dorsomedial crest [Figs. 10, 13, 14]), bony spines (on the snout, frontal, ventrolateral surface of head, upper and lower cleithral ring, subdorsal ridges, and principal trunk and tail ridges [Figs. 1–5] vs. absence of spines except on the snout in I. australae and I. larsonae [Figs. 12–13, 15]; four subdorsal spines, large cleithral ring spine at level of last pectoral-fin ray, and small spine present posterolaterally of the pelvic-fin base in I. lumnitzeri [Figs. 13–15]). Cylix tupareomanaia can be further distinguished from the members of Idiotropiscis by the number of subdorsal rings (3 vs. 4), tail rings (35–36 vs. 37 in I. australae, 39–40 in I. larsonae, 43 in I. lumnitzeri), and the tail rings
Fig. 15. µCT scanned skeleton of *Idiotopiscis lumnitzeri*, CAS HH-0423, male, 69.9 mm SL. (A) Osteocranium in lateral view highlighting the ventral cleithral cheek spine and small spine posteroventral of pectoral-fin base. (B) Subdorsal-fin base in lateral view highlighting the one upper and one lower subdorsal spines. Abbreviations: CS, cleithral spine; LSDS, lower subdorsal spine; PLS, posterolateral spine on pectoral-fin base; USDS, upper subdorsal spine.
Fig. 16. Lateral view of μCT scanned neurocranium of (A) Cylix tupareomanaia, NMNZ P.046322; (B) Hippocampus barbouri, USNM 220605. Abbreviations: ANP, anterior nuchal plate; CO, coronet on anterior nuchal plate; PNP, posterior nuchal plate; SC, supracleithrum; SOC, supraoccipital.

Fig. 17. Phylogenetic hypothesis using nuclear gene sequences TMO-4C4 and 18S retrieved with Maximum Likelihood (ML), Maximum Parsimony (MP), and Bayesian Inference (MrBayes), representing 17 species from clade 6 from the analysis of Hamilton et al. (2017) and the new taxon. Tree rooted with the southern Australian trunk-brooder pipefish Heraldia nocturna. Nodal support at the generic level is shown in ML/MP/MrBayes order. See Data Accessibility for tree file.
spanning the male brood pouch (8 vs. 10 in *I. australis*, 8 in *I. larsonae*, 10 in *I. lumnitzeri* [Table 4]).

The morphologically similar members of *Acentronura* (Figs. 8–9) share a number of characteristics of the head with *Cylix* and *Idiotropiscis*, including: the absence of anterior nuchal plate, presence of posterior nuchal plate, with large gap between it and the supraopercipital; presence of the bony dorsosmedial crest on the posterior nuchal plate; and fully enclosed male brood pouch enfolded by 7, 14, and 12 pouch plates in *A. breviperula*, *A. gracilissima*, and *A. tentaculata*, respectively (vs. 10 in *C. tupareomanaia* and 9–11 in *Idiotropiscis* [Table 4]). *Acentronura* can be distinguished by the slender trunk (vs. deep trunk), continuous superior trunk ridge (vs. discontinuous), low supraopercipital (vs. elevated supraopercipital), distinct and low dorsosmedial bony crest followed by a raised bony dimple on the supraopercipital (vs. prominent dorsosmedial bony crest protruding anteriorly in *Idiotropiscis*; and large cup-like pentamerous crest protruding anteriorly in *C. tupareomanaia*), presence of bilateral bony lobed protuberances on the posterolateral margins of the post-temporal bones (vs. present in *Idiotropiscis*; absent in *C. tupareomanaia*); absence of body spines (vs. snout spines in *I. australis* and *I. larsonae*; four subdorsal spines. large cleithral spine at level of last pectoral-fin ray, and small spine present posterolaterally on the pelvic-fin base in *I. lumnitzeri*; and spines on snout, frontal, ventrolaterally of head, upper and lower cleithral ring, subdorsal ridges, and principal trunk and tail ridges in *C. tupareomanaia*, number of tail rings (43 vs. 37 in *I. australis*, 39–40 in *I. larsonae*, 43 in *I. lumnitzeri*; 35–36 in *C. tupareomanaia* [Tables 3, 4]), and the number of tail rings spanning the male brood pouch (14 vs. 11 in *I. australis*, 9 in *I. larsonae*, 11 in *I. lumnitzeri*; 8 in *C. tupareomanaia* [Table 4]). The anteriormost plate is broad and paddle-shaped at the ventrocaudal margin and curved posterolaterally relative to the other plates, which are uniform in shape, in *A. gracilissima*, *A. tentaculata*, *I. australis*, and *I. lumnitzeri* (vs. all uniform in shape in *C. tupareomanaia*; unknown in *A. breviperula* and *I. larsonae*). The brood pouch is further distinguished in *A. gracilissima* by the first and second anteriormost pouch plates, which appear to be large and bifurcated ventrolateral extensions (Fig. 9B). Additionally, the congener *A. breviperula* shares the fully enclosed male brood pouch enfolded by arcuate ventrolateral bony extensions (Fig. 12, Table 4).

**Morphological comparisons to seahorses.**—*Cylix* and *Idiotropiscis* are superficially similar in appearance to members of *Hippocampus* and share with the latter numerous morphological synapomorphies, including meristic characters, an elevated frontal and supraopercipital, principal trunk ridge configuration, elevated dorsal-fin base, head angled ventrally relative to the principal body axis (25° vs. 90° in seahorses), moderately deep trunk (vs. slender trunk in *Acentronura*), male brood pouch, prehensile tail, and absence of a caudal fin. *Cylix tupareomanaia*, in particular, exhibits seahorse-like characteristics, including head and principal body ridge spines present on the snout, frontal, cleithral ring, and subdorsal area, and a highly derived supraopercipital crest present anterodorsally on its head that is remarkably similar in outward appearance to the distinct coronet present in most species of *Hippocampus* (Fig. 16, Table 5). In 2006, the first photographic record of *C. tupareomanaia*, observed in coralline and red algae at 10 m depth, was taken at Tawhiti Rahi, the Poor Knights Islands, Northland, New Zealand (Kuiter, 2009: 93, figs. A, B). However, the female individual in the photograph was originally misidentified as the subtropical Southwest Pacific seahorse, *Hippocampus jugumus* Kuiter, 2001, due to a superficial similarity in external appearance to this species (e.g., slender body, distinct coronet, continuous cleithral ring, and meristic characters) and therefore at the time mis-recorded as a range extension from its type locality of Lord Howe Island, NSW, Australia to temperate New Zealand. *Hippocampus jugumus* has since been collected from New Zealand waters, at the offshore subtropical Rangitāhua Kermadec Islands in the northernmost region of New Zealand (Clark et al., 2017).

Despite the similarity between *Cylix* and *Hippocampus*, a suite of anatomical features of the head and first trunk ring (Fig. 16, Table 5) readily distinguish *Cylix* from *Hippocampus*, including: anterior nuchal plate absent (vs. present in the modified form of a coronet in *Hippocampus* between the supraopercipital and the posterior nuchal plate); the elevated supraopercipital well separated from the cleithrum above the operculum, forming a large gap between the two areas (vs. supraopercipital and anterior and posterior nuchal plates interdigitated dorsally and connected lateroventrally by the cleithrum); distinct coronet present but derived from the cup-like and divided pentamerous bony crest on the supraopercipital bone (vs. derived from the modified anterior nuchal); presence of dorsosmedial bony crest on the posterior nuchal plate (vs. absence); cleithrum reaches mid-dorsally over anterior margins of bony dorsosmedial crest (vs. ventrally on a projected horizontal line through gills in members of *Hippocampus* with the exception of *H. jugumus* [Kuiter, 2001]) and the pygmy seahorse species *H. japapigu*, *H. pontothi*, *H. satomiae*, and *H. waleeanaus* [Short et al., 2018]); snout spines present on the mesethmoid and angled dorsally (vs. present directly anterior of the interorbital space and angled anteriorly); elevated rim of orbit protruding dorsally and ventrally (vs. no elevation of rim of orbit); eye spines absent (vs. presence of spines dorsally and ventrally of eye); strongly elevated ventrolateral bulge on first trunk ring supporting the pectoral fin (vs. absence of ventrolateral bulge on first trunk ring); and male brood pouch plates present (vs. absent).

**Genetic distances and phylogenetics.**—Table 6 summarizes uncorrected p-distances at the COX1 gene between *C. tupareomanaia* and the previously sequenced pygmy pipehorses *A. breviperula*, *A. tentaculata*, and *I. lumnitzeri* (Hamilton et al., 2017). *Cylix tupareomanaia* differs from *A. breviperula* by 19.5%, *A. tentaculata* by 20.4%, *I. australis* by 14.1%, and *I. lumnitzeri* by 18.4%.

Genetic analyses performed here using the nuclear gene sequences TMO-4C4 and 18S, and retrieved with ML, MP, and MrBayes (Fig. 17), resulted in well-supported topologies concordant with the hypothesized clade Vi of Hamilton et al. (2017). The pygmy pipefish genera *Cylix*, *Idiotropiscis*, and *Acentronura* form a monophyletic group with strong support in which *C. tupareomanaia* is placed as sister group to a clade comprising *Acentronura* and *Idiotropiscis*. Together, the three genera form the sister group to a clade comprising the Indo-Pacific pipefish genera *Filippicamp*, *Haliichthys*, *Lissocampus*, and *Trachyrhamphus*, all of which are endemic or occur in Australia and New Zealand. All of these aforementioned genera together form a clade representing the sister group to *Hippocampus*. The placement of *C. tupareomanaia* in clade Vi
Table 6. Uncorrected genetic distances (p-distances) summary between C. tupareomanaia and species of Acentronura and Idiotropiscis based on cytochrome c oxidase I (COI) sequences analyzed in this study.

| GenBank | Species          | 1   | 2   | 3   | 4   | 5   |
|---------|------------------|-----|-----|-----|-----|-----|
| 1       | KY066067         | A. breviperula |     |     |     |     |
| 2       | KY066068         | A. tentaculata | 0.144|     |     |     |
| 3       | MH306206         | C. tupareomanaia | 0.195| 0.204|     |     |
| 4       | MH306205         | I. australae   | 0.097| 0.131| 0.179|     |
| 5       | KY066120         | I. lumnitzeri  | 0.146| 0.146| 0.184| 0.141|

further supports the refutation by Hamilton et al. (2017) of the immediate sister taxon relationship between Hippocampus and the pygmy pipehorses hypothesized by Teske and Beheregaray (2009).

DATA ACCESSIBILITY

The tree file for the phylogenetic hypothesis associated with this work (Fig. 17) is available at https://www.ichthyologyandherpetology.org/i2020136. Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the DOI of the Iichthyology & Herpetology article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License. ZooBank publication urn:lsid:zoobank.org: pub:DD96034D-06EC-4FA5-9E68-B128195F88D3.

ACKNOWLEDGMENTS

We give sincere thanks to Hori Parata and kaumātua of Ngātiwai for the partnership with the Auckland Museum and in collaborating with the naming of Cylix tupareomanaia, and for sharing their mātauranga o Ngātiwai. This collaboration acknowledges Ngātiwai as kaitiaki (guardians) of Cylix tupareomanaia. We are grateful to Te Kahuratai Painting and Daniel Hikuroa, University of Auckland, for the thoughtful translation of the Abstract. Many individuals and institutions contributed in the field, laboratory, observations, and collegial discussions, and provided valuable specimens that served as the basis for this study. We would like to particularly thank Crispin and Irene Middleton for collecting and photographing a paratype specimen from the Cavalli Islands and the holotype at Waianapua Bay, Whangaruru; Andrew Stewart, Museum of New Zealand Te Papa Tongarewa, for providing access to the paratype specimen of C. tupareomanaia; Severine Hannam, Auckland Museum, for amazing curatorial assistance and collection efforts of the holotype specimen in northern New Zealand; special thanks to Kevin Conway, Texas A&M University, for editing the manuscript; Oliver Crimmen and Ralf Britz, Natural History Museum, London for assistance in providing x-ray radiographs of the holotypes of A. breviperula and A. tentaculata; David Catania, Jon Fong, and Mysi Hoang, California Academy of Sciences, for amazing curatorial assistance; Mark McGrouther, Amanda Hay, and Matt Lockett, Australian Museum, for amazing curatorial assistance and specimen loan of I. lumnitzeri; Ralph Foster, South Australian Museum, for specimen loan of I. australae; Glenn Moore, Western Australian Museum, for specimen loan of I. australae; Libby Liggins, Institute of Natural and Mathematical Sciences, Massey University, for providing COX1 sequences for C. tupareomanaia and the nuclear sequences 18S and TMO-4C4 for I. australae; Avery Hiley and Greg Rouse, Scripps Institution of Oceanography, UC San Diego, for providing the nuclear sequences 18S and TMO-4C4 for C. tupareomanaia; Michael Hammer, Museum and Art Gallery of the Northern Territory, for photographs and x-rays of I. larsoneae; Laith Jawad, Freelance Fish Consultant, and Claire Attenborough for providing x-rays of the type and comparative specimens; Adam Summers and Jules Chabain, Friday Harbor Laboratories, University of Washington, for high-resolution underwater photographs of C. tupareomanaia; Alison Perkins, underwater photographer, for underwater photographs and observations of C. tupareomanaia at the type location; Carey Harmer, Leafy Seadragon Tours, for many illuminating discussions on I. australae; Andrew Trevor-Jones, Australian Museum, for many illuminating discussions on I. lumnitzeri. Special thanks to David Harasti, Port Stephens Fisheries Institute, Louw Classans, Rhodes University, and Maarten De Brauwer, Curtin University, for their gushing support of all things syngnathids and lively discussions; and Greg Misner, Aoteaaro Hydrogen Alliance, for the generation of the geographic information system (GIS) map of the distribution of C. tupareomanaia within New Zealand. Finally, we would like to express gratitude for the work of C. E. Dawson, his classic 1985 book Indo-Pacific Pipefishes: Red Sea to the Americas provided a comprehensive assessment of syngnathid meristics and morphology for the genera Acentronura and Idiotropiscis, which proved invaluable for this study. The holotype and tail clipping from the type locality were collected under Fisheries New Zealand Special Permit number 691 issued to Auckland Museum. This research was supported in part by funding from NSF (DBI-1759637, DEB-170166) to Adam Summers, Friday Harbor Laboratories, University of Washington.

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### Appendix 1. GenBank numbers associated with mtDNA (COI) and nDNA (18S, TMO-4C4) sequences used in this study.

| Species                          | COI       | 18S       | TMO-4C4  | Reference                      |
|---------------------------------|-----------|-----------|----------|--------------------------------|
| Acentronura breviperula         | KY066067  | KY065694  | KY065608 | Hamilton et al., 2017          |
| Acentronura tentaculata         | KY066068  | KY065695  | KY065609 | Hamilton et al., 2017          |
| Cylix tupareomanaia, new species| MH306206  | MH286429  | MH286430 | This study                     |
| Filicampus tigris               | —         | KY065724  | KY065634 | Hamilton et al., 2017          |
| Halichthys taeniophorus         | —         | KY065729  | KY065639 | Hamilton et al., 2017          |
| Heraldia nocturna               | —         | KY065730  | KY065640 | Hamilton et al., 2017          |
| Hippocampus abdominalis         | —         | KY065731  | KY065641 | Hamilton et al., 2017          |
| Hippocampus bargibanti          | —         | KY065732  | KY065642 | Hamilton et al., 2017          |
| Hippocampus ingens              | —         | KY065734  | KY065645 | Hamilton et al., 2017          |
| Hippocampus kuda                | —         | KY065733  | KY065644 | Hamilton et al., 2017          |
| Hippocampus pontohi             | —         | KY065737  | KY065648 | Hamilton et al., 2017          |
| Hippocampus reidi               | —         | KY065739  | KY065650 | Hamilton et al., 2017          |
| Hippocampus trimaculatus        | —         | KY065740  | KY065651 | Hamilton et al., 2017          |
| Hippocampus whitei              | —         | KY065741  | KY065652 | Hamilton et al., 2017          |
| Hippocampus zosterae            | —         | KY065742  | KY065653 | Hamilton et al., 2017          |
| Idiotropiscis australis         | MH306205  | —         | —        | This study                     |
| Idiotropiscis lumnitzeri        | KY066120  | KY065746  | KY065657 | Hamilton et al., 2017          |
| Lissocampus caudalis            | —         | KY065749  | KY065660 | Hamilton et al., 2017          |
| Lissocampus runa                | —         | KY065750  | KY065661 | Hamilton et al., 2017          |
| Trachyrhamphus bicoarctatus     | —         | KY065781  | KY065687 | Hamilton et al., 2017          |

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