



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)

Authors: Short, Graham A., and Trnski, Thomas

Source: Ichthyology & Herpetology, 109(3) : 806-835

Published By: The American Society of Ichthyologists and Herpetologists

URL: <https://doi.org/10.1643/i2020136>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

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)

Graham A. Short^{1,2,3} and Thomas Trnski⁴

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 australe*, and *I. lumnitzeri* (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.

Ānei rā he puninga, he momo manaia iti hou. He uri nō Te Taitamawāhine, nō Te Taitokerau, arā, nō Aotearoa. Ko *Cylix tupareomanaia* tōna īngoa. He īngoa i tuku mai ā Ngāti Wai. Ka whakaahuatia tēnei manaia iti mai i ngā tīpako e toru (35.5–55.5 mitamano te roa paerewa). I kohia mai i te ākau tokatoka o te Te Taitokerau, 12–17 mita te hōhonu. He āhua ōrite ētahi o ngā āhuatanga o tēnei rōpū hou ki ngā puninga manaia taketake, ko *Acentronura*, nō Te Pāpaka-a-Māui/Ahitereiria, me tāna whanaunga, ko *Acentronura*, nō te rohe kotahi o Īnia me Te Moana-nui-a-Kiwa. Engari, ka taea te wetewetekiā a *Cylix tupareomanaia* pun. mo. hou mai i te āta tītiro ki ngā āhuatanga rerekē o ngā kōiwi, pērā i te putanga kōiwi mai i te angaanga, me kī, he tūpare. Ka taea te wetewetekiā hoki mai i ngā rerekētanga o ngā ira pata pūngao, arā ko te ira COX1 o ngā momo manaia it ko *Acentronura breviperula*, rātou ko *A. tentacula*, ko *Idiotropiscis australe*, ko *I. lumnitzeri*. Ka tautoko hoki te mātai iranga o ngā wāhi ira, 18S me TMO-4C4 ki tēnei whakapae whakapapa porī, hei rōpū whanaunga a *C. tupareomanaia*, momo hou, ki ngā puninga *Acentronura*, nga puninga *Idiotropiscis* hoki, arā, kotahi te tupuna o ēnei manaia katoa. Ko *Cylix tupareomanaia*, momo hou, te momo manaia iti tuawaru nō te tupuna manaia kotahi, nō te rohe kotahi o Īnia me Te Moana-nui-a-Kiwa kua whakaahuatia pēnei. Me kī, ko te tau 1921 kē te tau ki mua ka puta he pūrongo pēnei o tētahi puninga hou, momo hou hoki o te whānau manaia.

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 pipehorses, 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, thick plates of bony armor, and behavioral and morphological adaptations for crypsis.

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. blainvillaeus*, 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

¹ Department of Ichthyology, California Academy of Sciences, San Francisco, California 94118; Email: gshort@calacademy.org. Send reprint requests to this address.

² Ichthyology, Australian Museum Research Institute, Sydney NSW 2010, Australia.

³ Research Associate, Ichthyology, Burke Museum, Seattle, Washington.

⁴ Auckland War Memorial Museum Tāmaki Paenga Hira, Auckland 1142, New Zealand; Email: ttrnski@aucklandmuseum.com.

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

pipefish 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 australe* 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 *Amphelikturus* 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. australe* (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; Kuitert, 2004). *Idiotropiscis australe* 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. australe* 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. australe*, 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 re-described 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 Leysen (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 micro-computed tomography (μ CT) at the Karel F. Liem Bioimaging Facility (Friday Harbor Laboratories, University of Washington). Micro-computed tomography (μ CT) was performed using a Bruker Skyscan 1173 scanner (Billerica, MA) with a 1 mm aluminum filter at 60 kV and 110 μ A on a 2048 \times 2048 pixel CCD at a resolution of 8.8 μ m. 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 μ CT 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. australe* (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 supracleithrum; 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 *kylix*, 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-B1B8-6495E8886C05

Common Names: Māori—Tu pare o manaia, English—Manaia Pygmy Pipehorse
Figures 1–5, Tables 1–5

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

Acentronura australe: 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, Waitapau 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 Oturori 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*, *Lissonia*, 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 supraoccipital well behind the eye, height moderate, pentamerous in dorsal view, divided transversally into two concave sections (Figs. 3, 4); cleithral and supracleithral ridge prominent (Fig. 4); posterior margins of pentamerous 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, bilateral; rim of orbit with prominent dorsolateral and ventral ridges, fluted with rugose sculpturing; opercular ridge



Fig. 1. *Cylix tupareomanaia*. (A) AIM MA122274, female, holotype shortly after death, 31.4 mm SL; Waiatapu 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).

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; dorsum 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 symphysis 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. 2. *Cylix tupareomanaia*. (A) AIM MA122274, female, preserved holotype, 31.4 mm SL; Waitapaua Bay, Whangaruru, Northland, New Zealand (photograph © Auckland Museum). (B) NMNZ P.056154, female, preserved paratype, 35.5 mm SL; Cavalli Islands, Northland, New Zealand (photograph © Auckland Museum). (C) NMNZ P.046322, male, preserved paratype, 55.5 mm SL; east of Oturori Rock, Bay of Islands, Northland, New Zealand (photograph Graham Short).

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 3rd, 6th, 10th, 11th, and 12th rings, all bearing dermal flaps; lateral trunk ridges with

moderate-sized spines on each trunk ring starting at 2nd ring with enlarged spines on 3rd, 6th, and 10th rings; inferior trunk ridges with moderate-sized spines starting at 3rd ring with enlarged spines on 3rd, 6th, and 10th rings; subdorsal spines four, superior trunk ridge ending with two subdorsal spines,

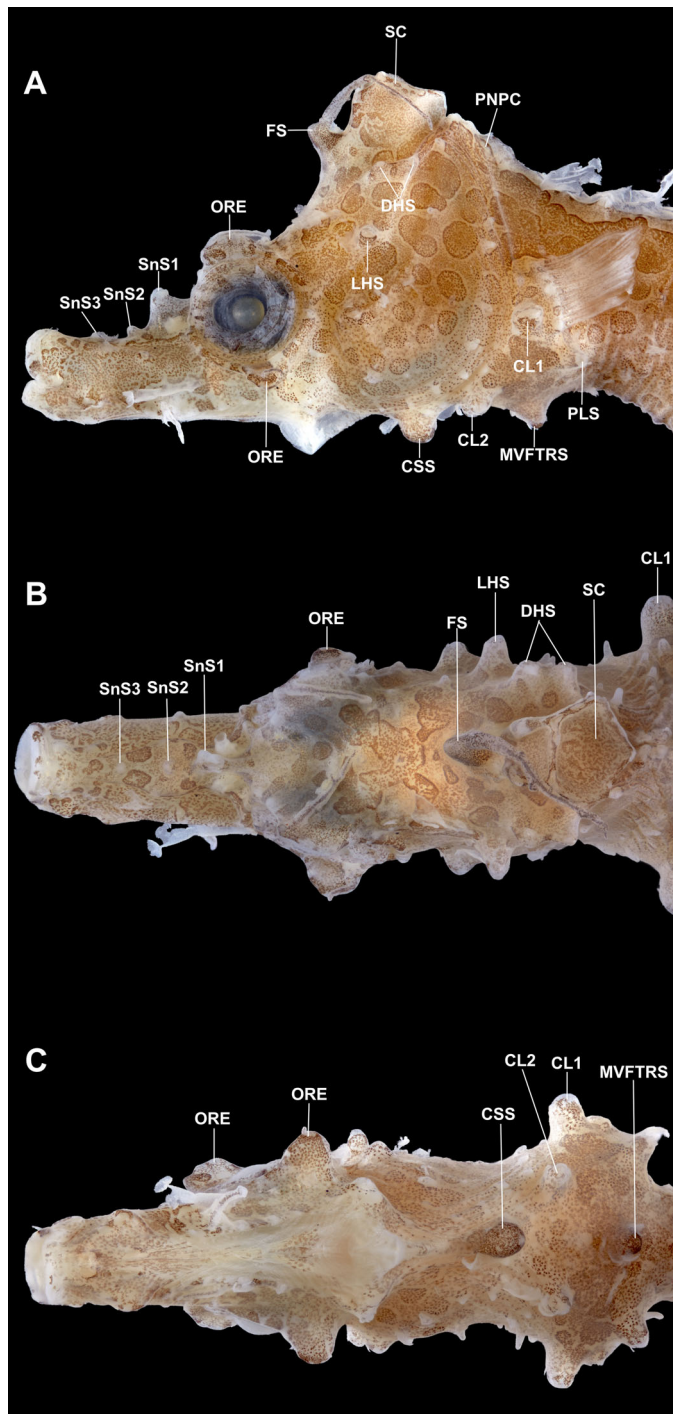


Fig. 3. Head of *Cylix tupareomanaia* (AIM MA122274, female, preserved holotype, 31.4 mm SL) in lateral (A), dorsal (B), and ventral (C) view highlighting positions of diagnostic characters, including the cup-like supraoccipital crest present on the supraoccipital, and large medioventral conical spines on the cleithral symphysis and the first trunk ring between the pectoral-fin bases. Abbreviations: CL, cleithral spines; CSS, medioventral conical spine on the cleithral symphysis; DHS, double head spine; FS, frontal spine; LHS, lateral head spine; MVFTRS, medioventral first trunk ring spine between the pectoral-fin bases; ORE, orbital rim extension; PLS, posterolateral spine on pectoral-fin base; PNPC, posterior nuchal plate crest; SC, supraoccipital crest; SnS, snout 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. Fleishy 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 Pēwhairangi (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

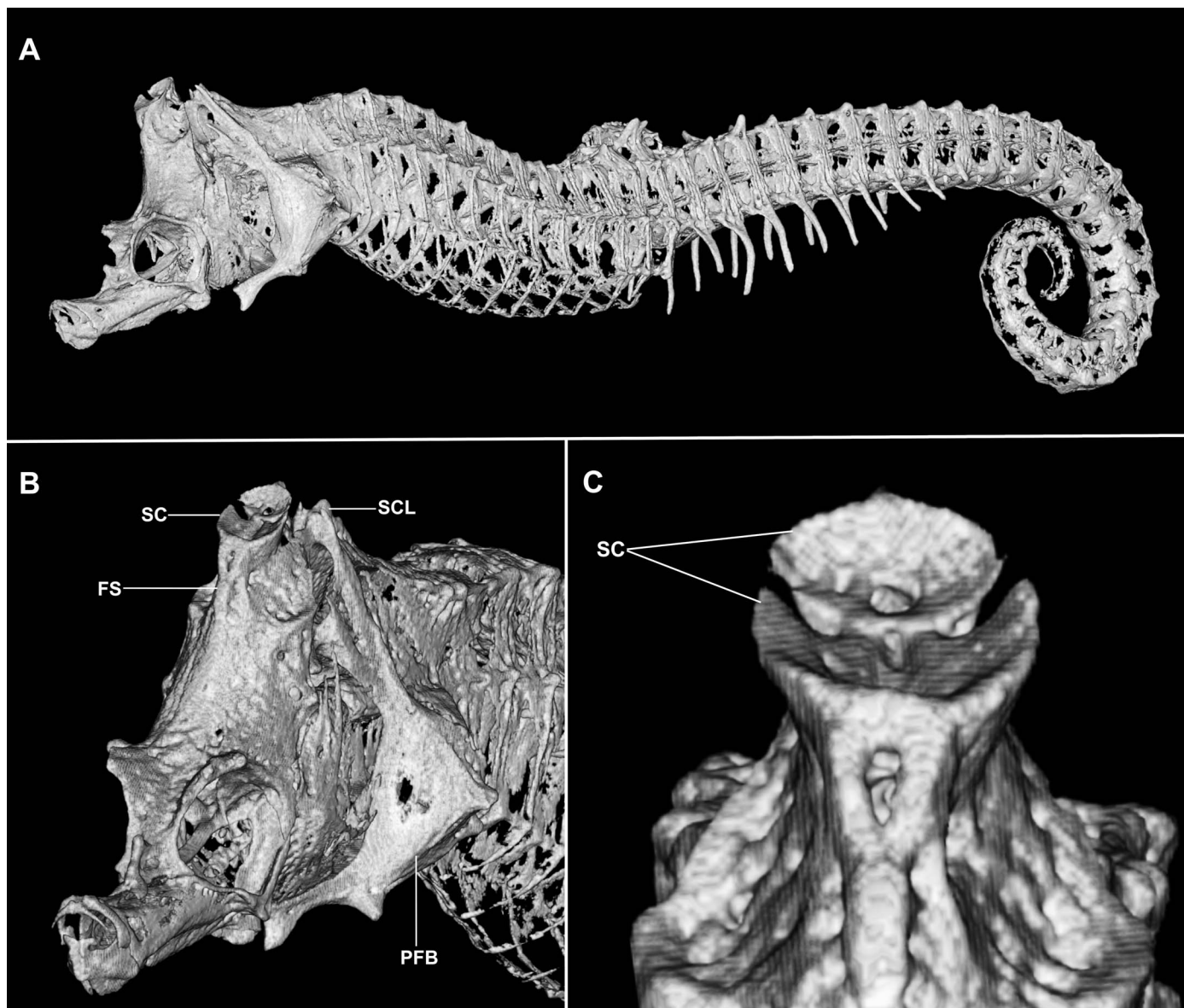


Fig. 4. μ CT scan of *Cylix tupareomanaia*, NMNZ P.046322, male, paratype, 55.5 mm SL. (A, B) Anterolateral view of the head highlighting the bifurcated and cup-like crest present on the supraoccipital, continuous cleithral ring, and the strongly elevated ventrolateral bulge of the pectoral-fin base. (C) Anterodorsal aspect of the neurocranium highlighting the bifurcated and cup-like pentamerous bony crest present on the supraoccipital. Abbreviations: FS, frontal spine; PFB, pectoral-fin base; SC, supraoccipital crest; SCL, supraclathrum.

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 *Chrysochrysis 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 Manawatāwhi 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).

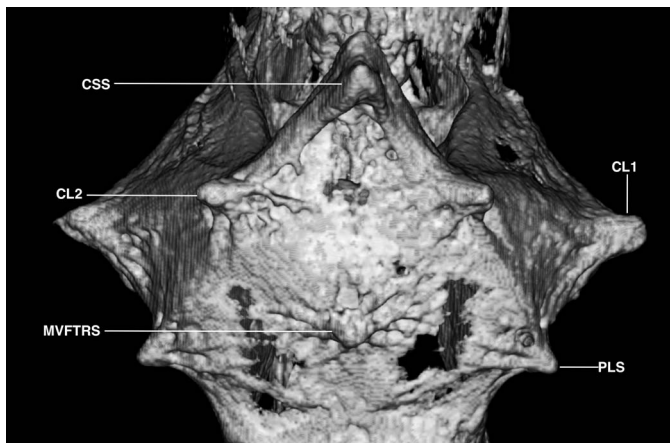


Fig. 5. μ CT scan of the ventral aspect of first trunk ring of *Cylix tupareomanaia*, NMNZ P.046322, male, paratype, 55.5 mm SL, in ventral aspect highlighting positions of large medioventral conical spines on the cleithral symphysis and the first trunk ring between the pectoral-fin bases. Abbreviations: CL, cleithral spines; CSS, medioventral conical spine on the cleithral symphysis; MVFTRS, medioventral first trunk ring spine between the pectoral-fin bases; PLS, posterolateral spine on pectoral-fin base.

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 Manawatāwhi 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).

	<i>Cylix tupareomanaia</i>	<i>Cylix tupareomanaia</i>	<i>Cylix tupareomanaia</i>
Voucher number	AIM MA122274	NMNZ P.046322	NMNZ P.056154
Type	Holotype	Paratype	Paratype
SL (mm)	31.4	60.6	39.9
Trunk rings	13	13	14
Tail rings	36	35	36
Subdorsal trunk rings	3	3	3
Dorsal-fin rays	14	14	14
Anal-fin rays	4	4	4
Pectoral-fin rays	14	14	14
HL:SL	19.6	14.9	15.6
TrL:SL	28.4	26.6	30.8
DL:SL	5.3	5.8	5.76
PL:SL	3.12	3.0	3.1
TaL:SL	52.2	58.6	53.6
TD4:SL	7.7	8.9	7.30
TD9:SL	6.8	6.9	6.9
SnD:SnL	52.5	55.7	40.2
HD:HL	59.3	67.7	60.8
SnL:HL	32.6	42.1	39.2
OD:HL	16.3	15.7	19.4
PO:HL	42.7	40.0	43.5
CH:HL	48.2	52.6	52.2
HL:TrL	69.2	55.8	50.6

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	<i>C. tupareomanaia</i> , new species			<i>I. australe</i>	
	HT	PT	PT	NT	NT
Type	HT	PT	PT	NT	NT
Voucher number	AIM MA122274	NMNZ P.046322	NMNZ P.056154	WAM P.33543001	SAMA F2657
Trunk rings	13	13	14	13	13
Tail rings	36	35	36	37	37
Subdorsal trunk rings	3	3	3	4	4
Dorsal-fin rays	14	14	14	16	16
Pectoral-fin rays	14	14	14	15	16
Head angled ventrad 25°	Present	Present	Present	Present	Present
Superior and inferior trunk and tail ridges	Discontinuous	Discontinuous	Discontinuous	Discontinuous	Discontinuous
Cup-like crest on supraoccipital	Present	Present	Present	Absent	Absent
Dorsomedial bony crest on supraoccipital	Absent	Absent	Absent	Present	Present
Dorsomedial bony crest on first trunk ring	Present	Present	Present	Present	Present
Bilateral protuberances present lateroposteriorly on posttemporal	Absent	Absent	Absent	Present	Present
Large rugose lateral head spine	Present	Present	Present	Absent	Absent
3 small lateral head spines	Present	Present	Present	Absent	Absent
Frontal spine	Present	Present	Present	Absent	Absent
Snout spines	Present	Present	Present	Present	Present
Midventral conical spines on cleithral symphysis and first trunk ring	Present	Present	Present	Absent	Absent
Cleithral ring confluent	Present	Present	Present	Absent	Absent
Cleithral ring spine on pectoral-fin base	Present	Present	Present	Absent	Absent
Cleithral ring spine ventrally of first trunk ring	Present	Present	Present	Absent	Absent
Small spine ventroposteriorly of pectoral-fin base	Present	Present	Present	Absent	Absent
Subdorsal spines	Present	Present	Present	Absent	Absent
Orbital rim extension	Present	Present	Present	Present	Present
Swelling of gular region ventroposterior to eye	Present	Present	Present	Present	Present
Superior trunk ridge spines	3, 6, 10			Absent	Absent
Superior tail ridge spines	4, 7, 11			Absent	Absent
Anal-fin	Present	Present	Present	Present	Present

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

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	<i>C. tupareomanaia</i>	<i>A. breviperula</i>	<i>A. gracilissima</i>	<i>A. tentaculata</i>	<i>I. australe</i>	<i>I. larsonae</i>	<i>I. lumnitzeri</i>
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 I.38660-001
Type	Paratype	Holotype	Non-type	Holotype	Non-type	Holotype	Holotype
Trunk rings	8	7	14	12	10	8	11

Table 3. Extended.

<i>I. larsonae</i>		<i>I. lumnitzeri</i>		<i>A. breviperula</i>	<i>A. gracilissima</i>	<i>A. tentaculata</i>	
HT	PT	NT	NT	NT	NT	NT	NT
NTM	GCRL	CAS	AMS	CAS	CAS-SU	CAS	CAS
S.10805-001	21518	HH-0423	I.45395-001	247135	6681	247139	247139
11	11	11	11	12	13	12	12
39	40	45	43	42	45	44	43
4	4	4	4	4	4	4	4
17	17	15	15	15	16	16	16
12	13	13	13	14	15	14	14
Present	Present	Present	Present	Present	Present	Present	Present
Discontinuous	Discontinuous	Discontinuous	Discontinuous	Continuous	Continuous	Continuous	Continuous
Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Present	Present	Present	Present	Present	Present	Present	Present
Present	Present	Present	Present	Present	Present	Present	Present
Present	Present	Present	Present	Present	Present	Present	Present
Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Absent	Absent	Present	Present	Absent	Absent	Absent	Absent
Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Absent	Absent	Present	Present	Absent	Absent	Absent	Absent
Absent	Absent	Present	Present	Absent	Absent	Absent	Absent
Absent	Absent	Present	Present	Absent	Absent	Absent	Absent
Present	Present	Present	Present	Absent	Absent	Absent	Absent
Absent	Absent	6, 10		Absent	Absent	Absent	Absent
Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Present	Present	Present	Present	Present	Present	Present	Present

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

Species	<i>Hippocampus</i> spp.	<i>C. tupareomanaia</i>	<i>I. australe</i>	<i>I. larsonae</i>	<i>I. lumnitzeri</i>
Coronet	Present	Present	Absent	Absent	Absent
Subdorsal rings 4	Present	Present	Present	Present	Present
Parietal spine	Present	Present	Absent	Absent	Absent
Lateral head spines ventral of coronet	Present	Present	Absent	Absent	Absent
Snout spine	Present	Present	Present	Present	Absent
Cleithral ring spines	Present	Present	Absent	Absent	Present
Subdorsal spines	Present	Present	Absent	Absent	Present
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	Present

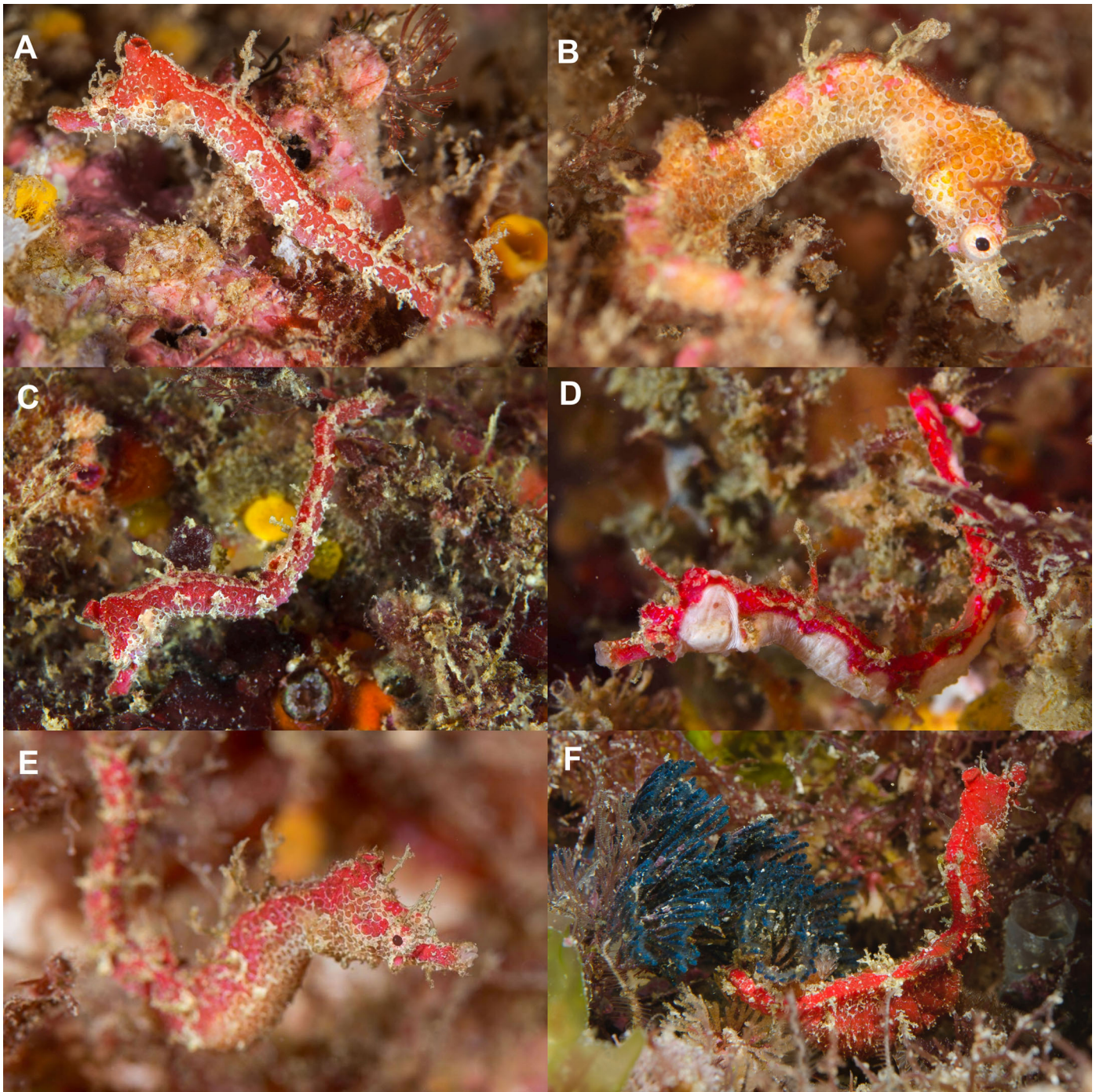


Fig. 6. *Cylix tupareomanaia* in situ. (A) AIM MA122274, female, holotype, Waitapaua Bay, Whangaruru, Northland, New Zealand, 12 m depth (photograph © Shane Housham). (B) Waitapaua Bay, Whangaruru, Northland, New Zealand, 12 m depth (photograph © Shane Housham). (C) Waitapaua Bay, Whangaruru, Northland, New Zealand, 12 m depth (photograph © Richard Smith). (D) Waitapaua Bay, Whangaruru, Northland, New Zealand, 12 m depth (photograph © Irene Middleton). (E) Waitapaua 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).

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. 7. Distribution of *Cylix tupareo-maia* in Taitokerau Northland, North Island, New Zealand. Square = type locality of holotype AIM MA122274 at Waitatapua Bay, Whangaruru. Star = locality of paratype NMNZ P.056154, Cavalli Islands. Circle = locality of paratype NMNZ P.046322, east of Oturori Rock, Bay of Islands. Arrow = specimen photographed at Poor Knights Islands.

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; bilateral bony lobed protuberances on the posterolateral margins of the post-temporal bones (Fig. 10A); anterior nuchal plate absent (Fig. 9A); posterior nuchal plate present anterior to cleithrum with dorsomedial crest-like ridge along its dorsum, large gap 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 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 breviperula* exhibits strong sexual dimorphism associated with the presence of a brood pouch. The brood pouch is formed along the ventral midline of the tail and is present below the anteriormost eight tail rings (Fig. 11A).

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; Kuitert, 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.

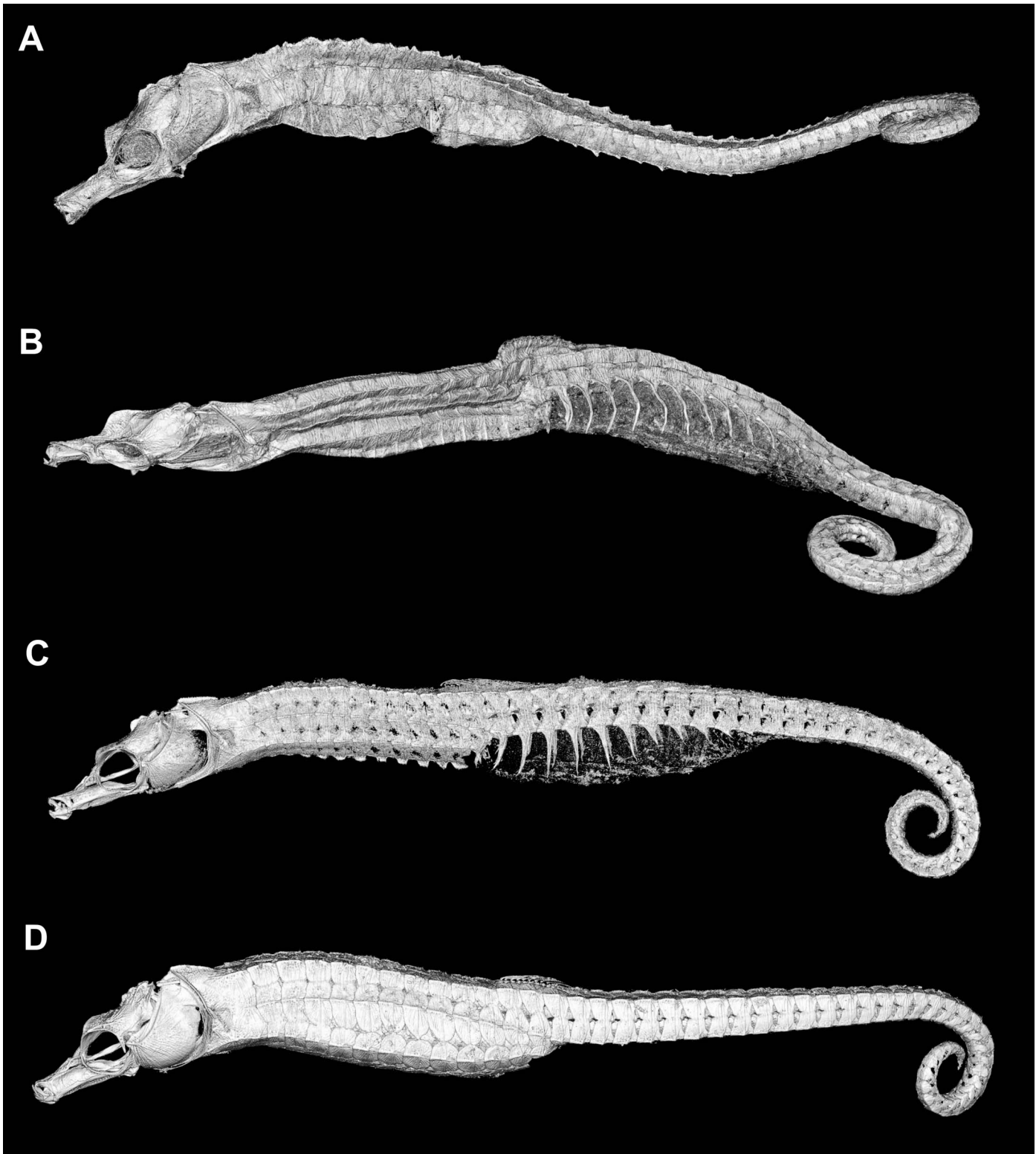


Fig. 9. Lateral view of μ CT scanned skeletons of preserved specimens of *Acentronura* spp. redescribed in this study. (A) *A. breviperula*, CAS 247135, female, 40.1 mm SL. (B) *A. gracilissima*, CAS-SU 6681, male, 70.4 mm SL. (C) *A. tentaculata*, CAS 247139, male, 50.8 mm SL. (D) *A. tentaculata*, 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

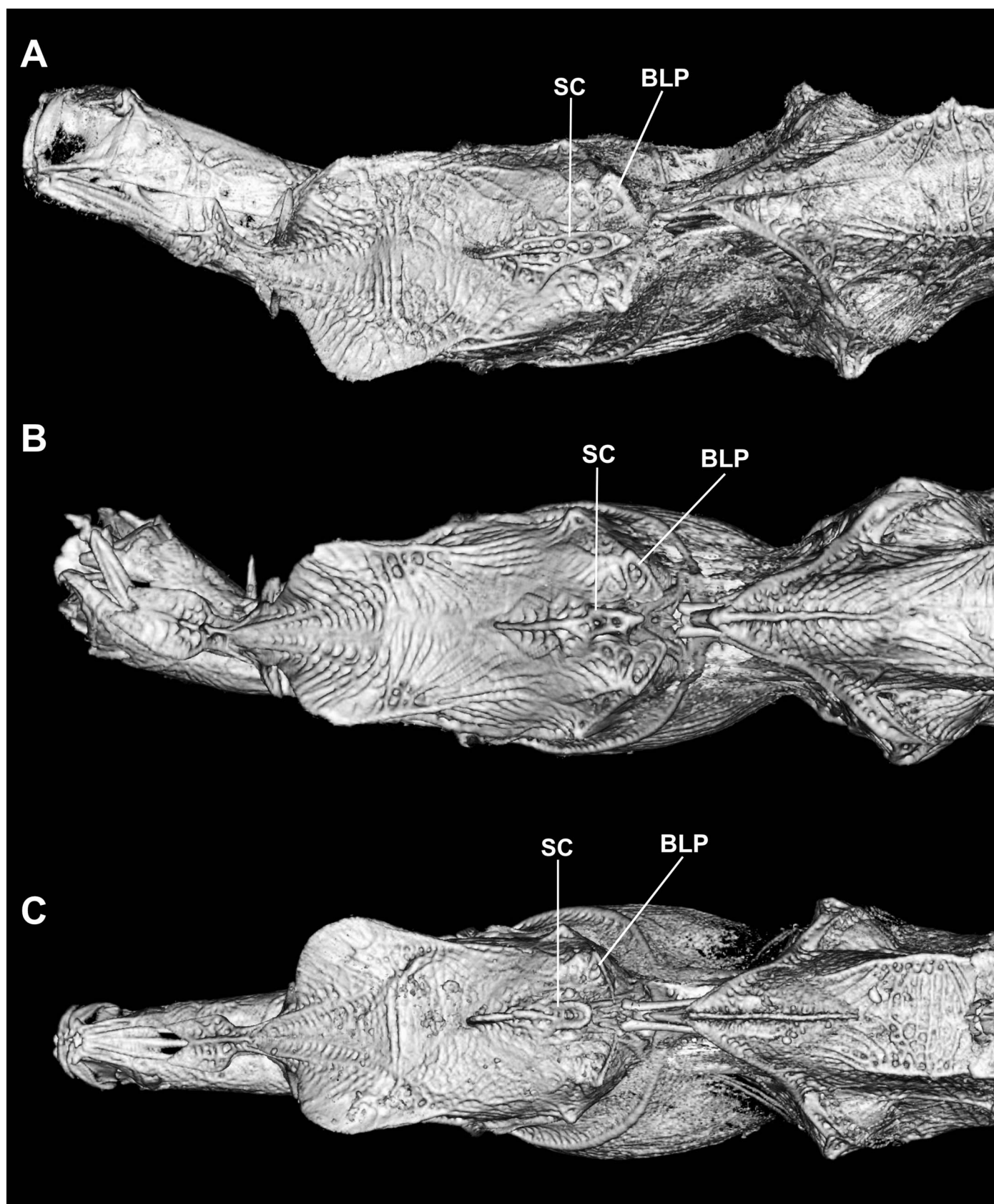


Fig. 10. Dorsal view of μ CT scanned neurocranium of (A) *Acentronura breviperulea*, CAS 247135, female; (B) *Acentronura gracilissima*, CAS 247139, male; (C) *Acentronura tentaculata*, CAS-SU 6681, male. Abbreviations: BLP, bilateral lobed protuberances; SC, supraoccipital crest.

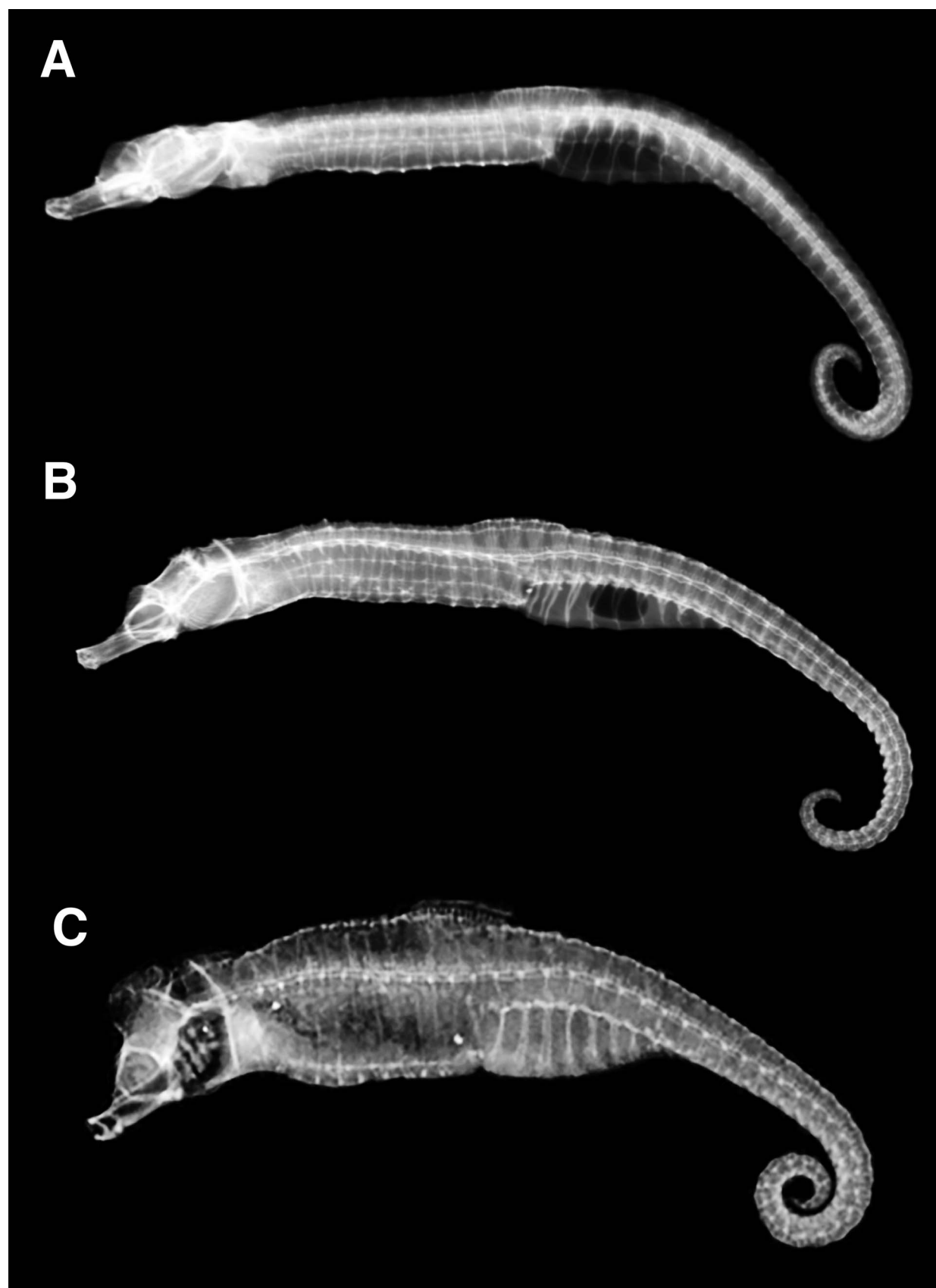


Fig. 11. X-ray radiography of (A) *A. breviperula*, BMNH 1890.1.14.51, male, holotype; (B) *A. tentaculata*, BMNH 1869.6.21.7, male, holotype; (C) *I. larsonae*, NTM S.10805-001, male, holotype, 55.5 mm SL (Photograph credits for *A. breviperula* and *A. tentaculata* to Oliver Crimmen and Ralf Britz, © 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). μ 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, Indochina, 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 Fourmanoir, 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: supraoccipital 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.

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 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 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 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). μ 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.

***Idiotropiscis* 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: supraoccipital is elevated with a distinct and raised bony dorsomedial crest; posterolateral margins of post-temporal bones expanded

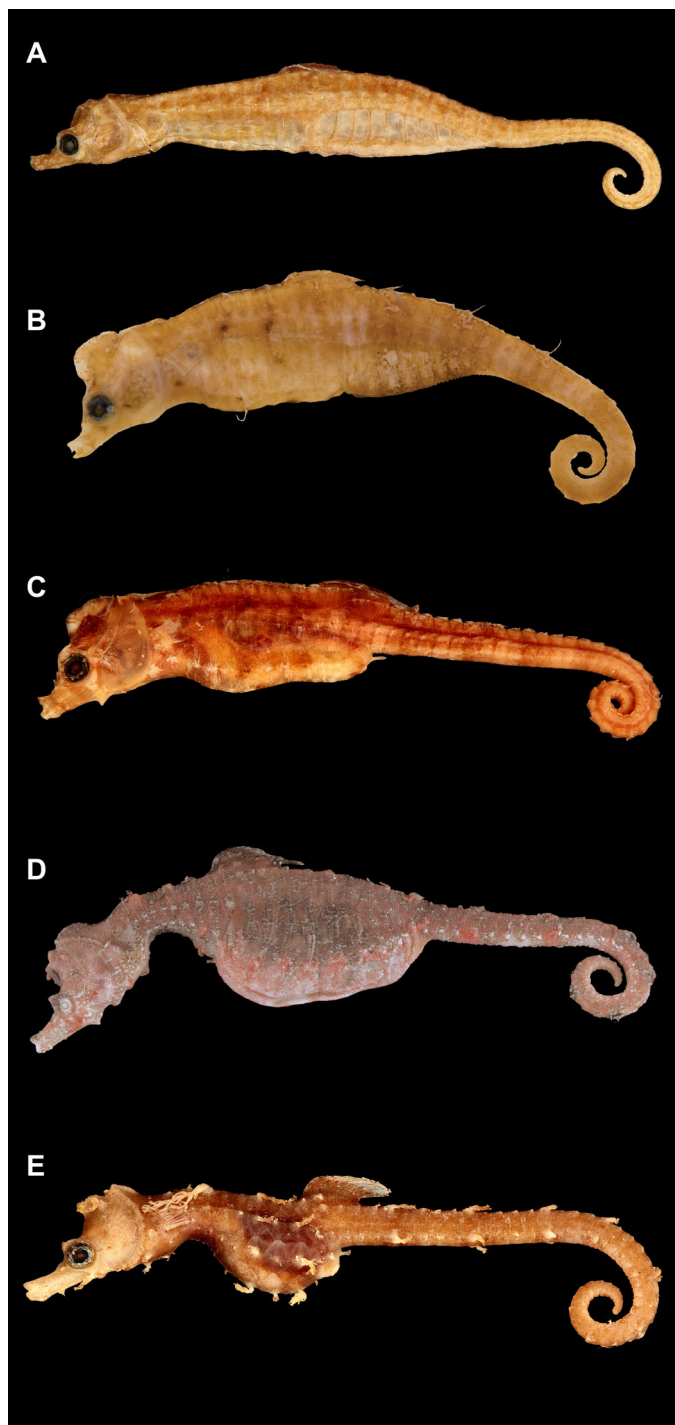


Fig. 12. Lateral view of preserved specimens of *Idiotropiscis* spp. redescribed in this study. (A) *I. australe*, WAM P.33543-001, male, 54.7 mm SL. (B) *I. larsonae*, NTM S.10805-001, male, holotype, 33.5 SL. (C) *I. larsonae*, GCRL 21518, female, paratype, 33.0 mm SL. (D) *I. lumnitzeri*, CAS HH-0423, male, 69.9 mm SL. (E) *I. lumnitzeri*, AMS I.45395-001, female, 54.0 mm SL.

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 australe* (Waite and Hale, 1921)**

Figures 12, 13; Tables 2–5

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

Diagnosis.—See generic diagnosis. *Idiotropiscis australe* 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 australe* 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). μ CT 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 australe* is endemic to the temperate waters of southern and southwestern Australia, from

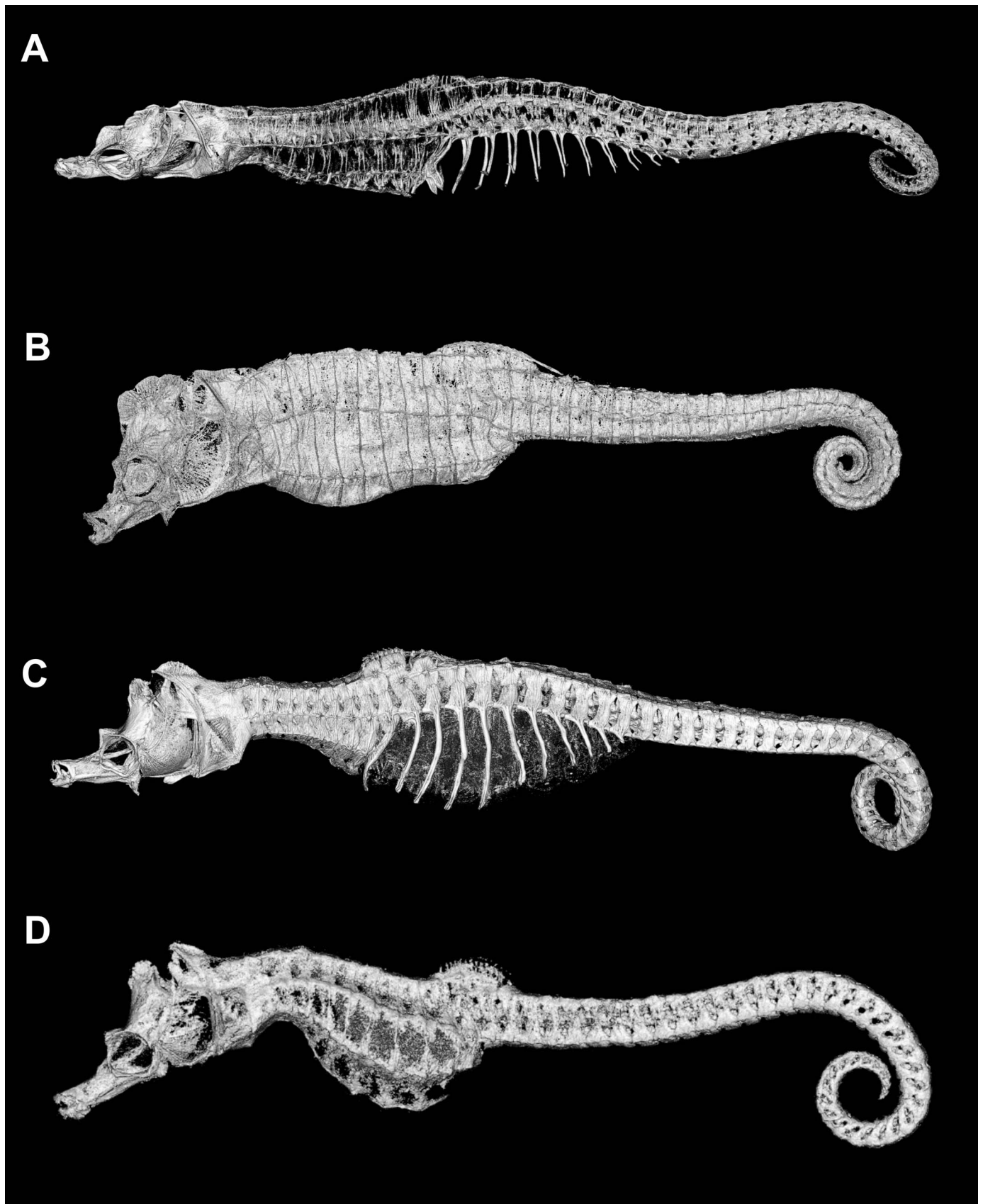


Fig. 13. Lateral view of μ CT scanned skeletons of preserved specimens of *Idiotropiscis* spp. redescribed in this study. (A) *I. australe*, WAM P.33543-001, male, 54.7 mm SL. (B) *I. larsonae*, GCRL 21518, female, paratype, 33.0 mm SL. (C) *I. lumnitzeri*, CAS HH-0423, male, 69.9 mm SL. (D) *I. lumnitzeri*, AMS I.45395-001, female, 54.0 mm SL.

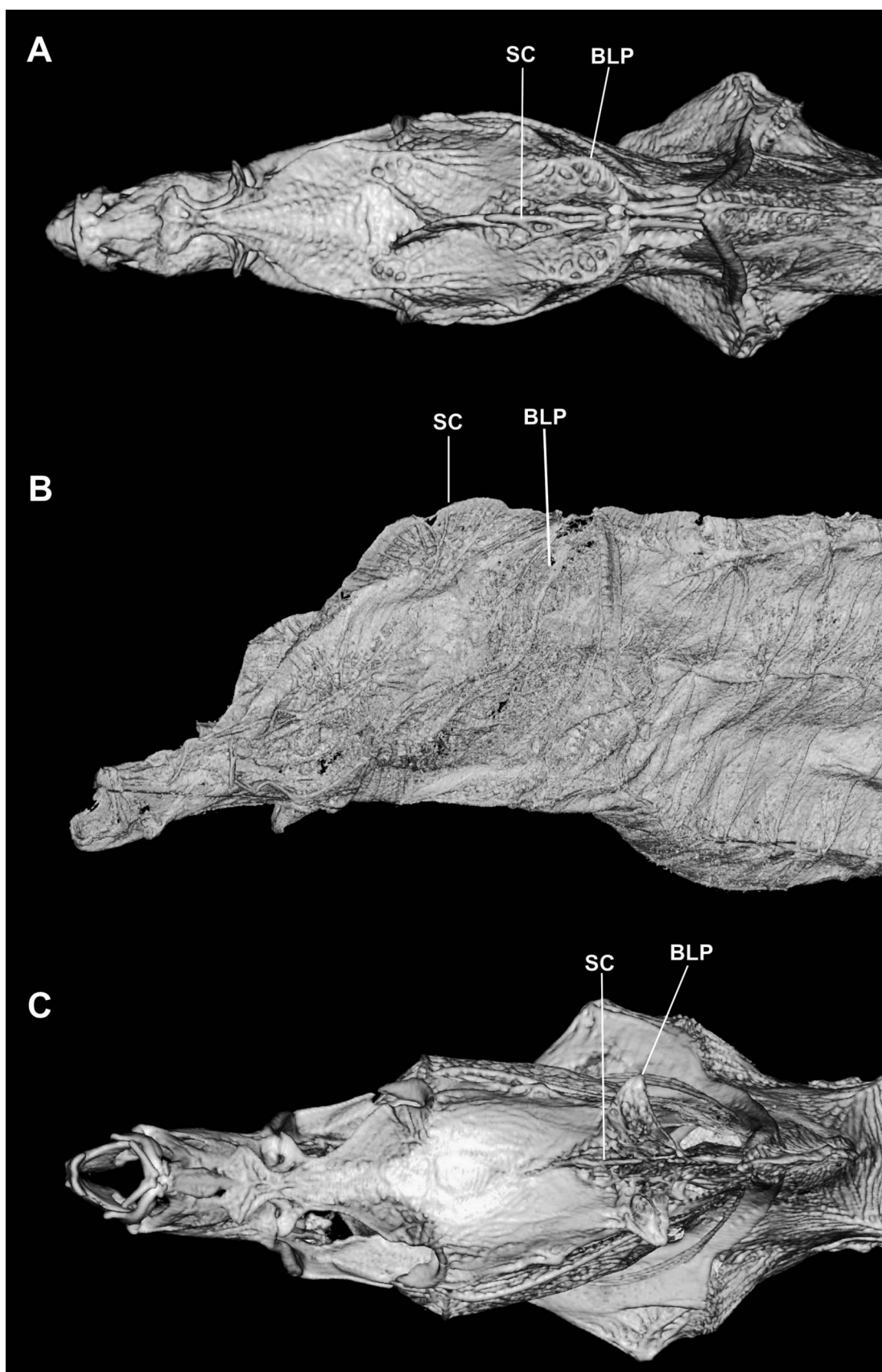


Fig. 14. Dorsal view of μ CT scanned neurocranium of the head of (A) *Idiotropiscis australe*, WAM P.33543-001, male; (B) *Idiotropiscis larsonae*, GCRL 21518, male; (C) *Idiotropiscis lumnitzeri*, CAS HH-0423, male. Abbreviations: BLP, bilateral lobed protuberances; SC, supraoccipital crest.

Cape Jarvis and the Gulf St Vincent, South Australia, and Carnac Island, Western Australia (Dawson, 1985).

Material examined.—*Idiotropiscis australe*: SAMA F2657, Yanakillilla, 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 and difficult to discern (Fig. 14B); 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; median dorsal snout spine present on mesethmoid bone; interorbital narrow, depressed; rim of orbit projecting moderately dorsolaterally and ventrally; opercular ridge low, entire, angled dorsally toward gill opening; swelling of the gular region ventroposteriorly of eye absent; pectoral-fin base without distinct ridges, low, strongly elevated ventrolateral bulge supporting the pectoral-fin base absent; trunk compressed laterally, span of dorsum of pre-dorsal trunk rings less by half of dorsum of anterior post-dorsal tail rings, span of trunk at lateral and inferior ridges somewhat greater than

span of dorsum of trunk; subdorsal rings four (spans three trunk rings and one tail rings vs. two trunk rings and two tail rings in paratype); principal body ridges distinct; superior tail ridge with slightly enlarged spines on 4th, 12th, and 16th trunk rings. Caudal fin absent.

Idiotropiscis larsonae exhibits strong sexual dimorphism associated with the presence of a brood pouch in the male (Figs. 11C, 12B). The brood pouch is formed along the ventral midline of the tail and is present below the anterior-most nine tail rings. X-ray image of the holotype revealed the brood pouch is enclosed by nine arcuate bony extensions and reduced in size posteriorly. The female paratype exhibits well-developed ossification of the skeleton, including the strong ossification of the inferior and ventral trunk area as detected by μ CT scanning (Fig. 13B).

Distribution.—*Idiotropiscis larsonae* is known only from the tropical waters of the Monte Bello Islands, north Western Australia (Dawson, 1985).

Material examined.—*Idiotropiscis larsonae*: NTM S.10805-001, adult male, holotype, Monte Bello Islands, Western Australia, Australia, 20°36'S, 115°37'E, depth 3–9 m, 22 April 1983; GCRL 21518, female, paratype, 33.0 mm SL, Monte Bello Islands, Western Australia, Australia, 20°36'S, 115°37'E, depth 3–9 m, 22 April 1983.

***Idiotropiscis lumnitzeri* Kuitert, 2004**

Figures 12–13, 15; Tables 2–5

Idiotropiscis lumnitzeri Kuitert, 2004: 165, fig. 1 (Henrietta Head, La Perouse, Sydney, New South Wales, Australia); AMS I.38660-001 (holotype).

Diagnosis.—See generic diagnosis. *Idiotropiscis lumnitzeri* differs from its congeners by the following combination of characters: strongly elevated 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; 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 spines: large spine present on cleithral ring at level of last pectoral-fin ray (Fig. 15A); small spine present posterolateral to the pelvic fin (Fig. 15A); 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 (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 I.45395-001) exhibits well-developed ossification of the skeleton, including the strong ossification of the inferior and ventral trunk area as detected by μ CT scanning (Fig. 13D). *Idiotropiscis lummitzeri* 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). μ CT 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 lummitzeri* 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 lummitzeri*: AMS I.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 pipehorses.—*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. australe* 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. lummitzeri* [Fig. 14]).

Cylix tupareomanaia differs primarily from the members of *Idiotropiscis* by features of the crest morphology on the supraoccipital bone (cup-like pentamerous 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 supracleithrum that extends dorsally from the cleithrum, forming a continuous bony collar (Fig. 5) vs. absence of a supracleithrum 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. australe* 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. lummitzeri* [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. australe*, 39–40 in *I. larsonae*, 43 in *I. lummitzeri*), and the tail rings

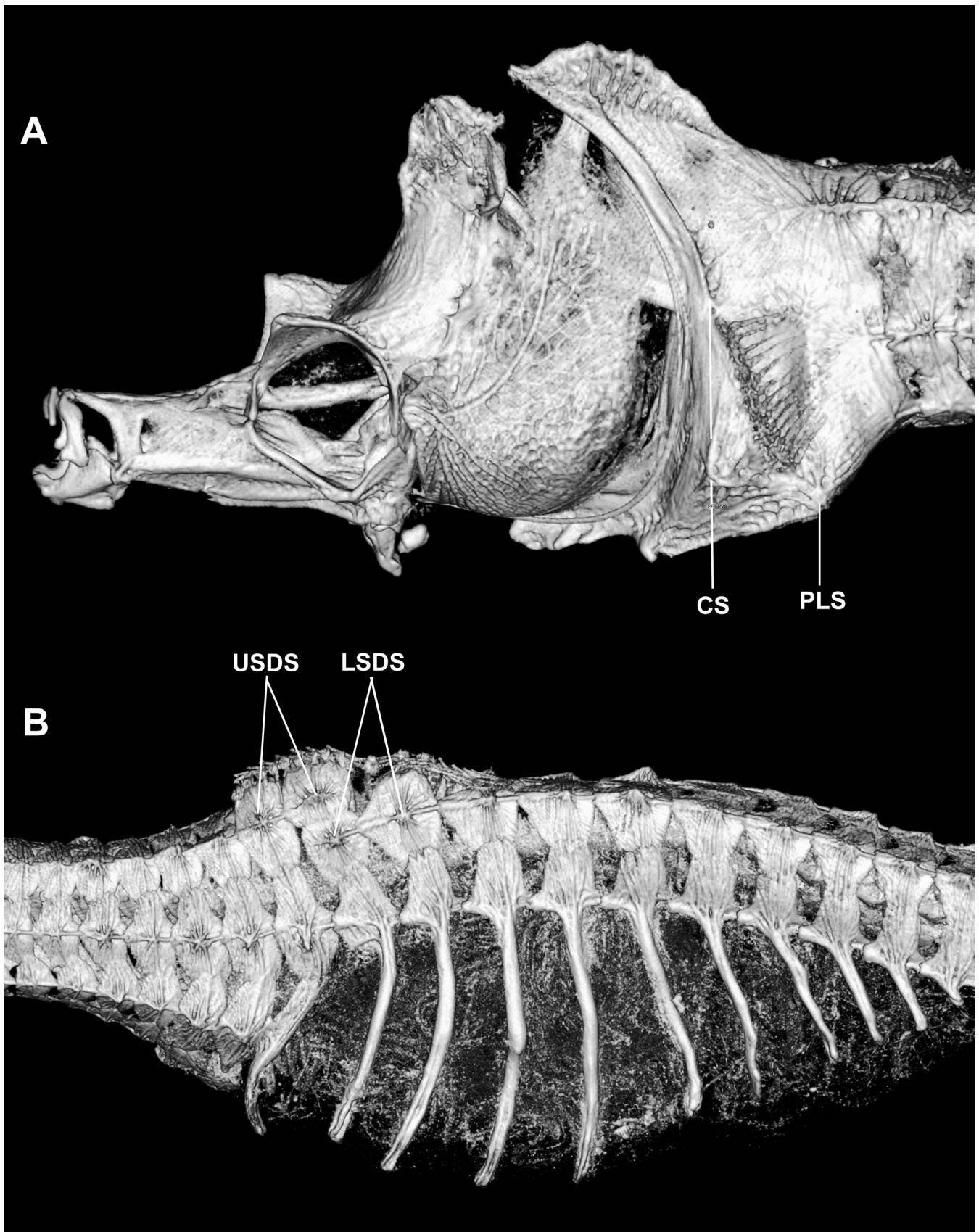


Fig. 15. μ CT scanned skeleton of *Idiotropiscis lumnitzeri*, CAS HH-0423, male, 69.9 mm SL. (A) Osteocranium in lateral view highlighting the ventral cleithral cheek spine and small spine posteroventral of pectoral-fin base. (B) Subdorsal-fin base in lateral view highlighting the one upper and one lower subdorsal spines. Abbreviations: CS, cleithral spine; LSDS, lower subdorsal spine; PLS, posterolateral spine on pectoral-fin base; USDS, upper subdorsal spine.

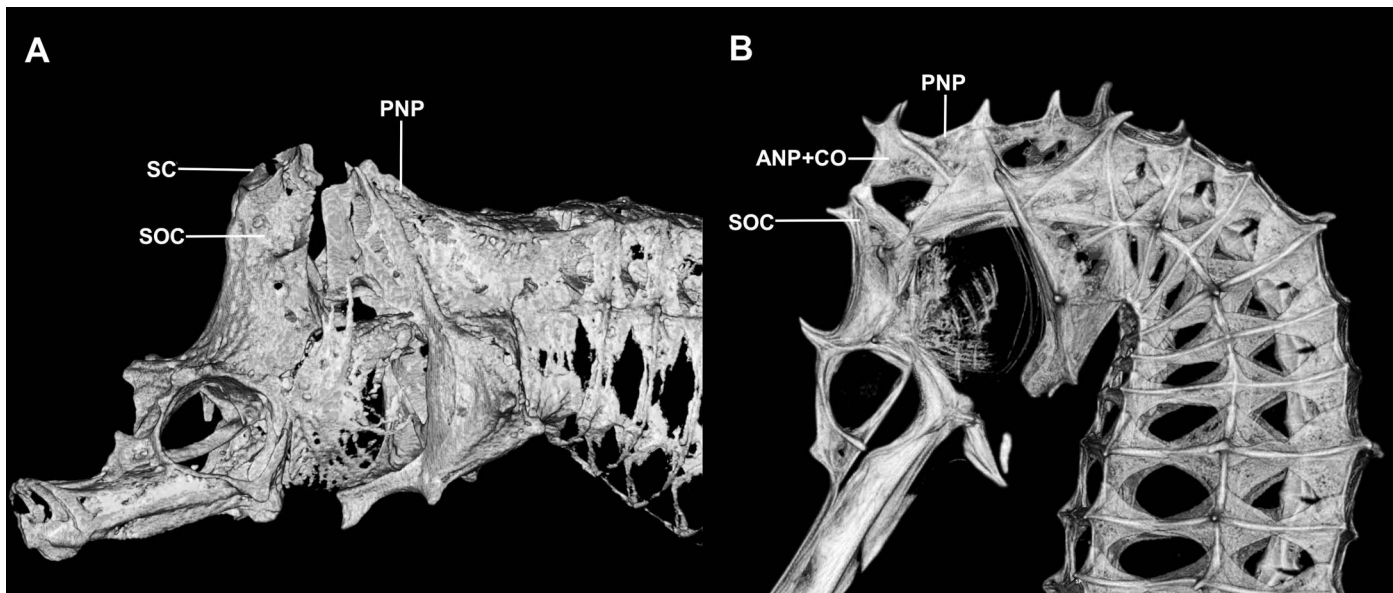


Fig. 16. Lateral view of μ CT scanned neurocranium of (A) *Cylix tupareomanaia*, NMNZ P.046322; (B) *Hippocampus barboursi*, USNM 220605. Abbreviations: ANP, anterior nuchal plate; CO, coronet on anterior nuchal plate; PNP, posterior nuchal plate; SC, supracleithrum; SOC, supraoccipital.

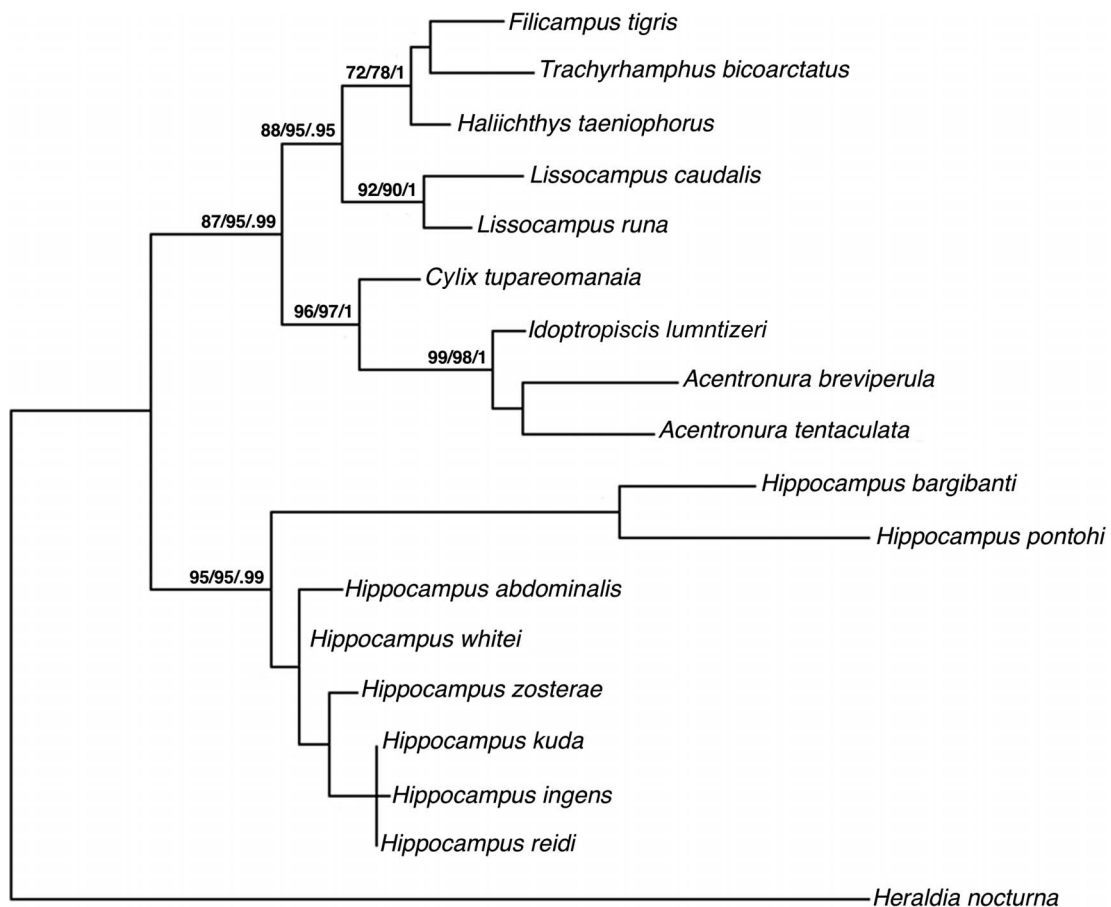


Fig. 17. Phylogenetic hypothesis using nuclear gene sequences TMO-4C4 and 18S retrieved with Maximum Likelihood (ML), Maximum Parsimony (MP), and Bayesian Inference (MrBayes), representing 17 species from clade 6 from the analysis of Hamilton et al. (2017) and the new taxon. Tree rooted with the southern 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. australe*, 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 supraoccipital; presence of the bony dorsomedial 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 slim trunk (vs. deep trunk), continuous superior trunk ridge (vs. discontinuous), low supraoccipital (vs. elevated supraoccipital), distinct and low dorsomedial bony crest followed by a raised bony dimple on the supraoccipital (vs. prominent dorsomedial 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. australe* 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. australe*, 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. australe*, 9 in *I. larsonae*, 11 in *I. lumnitzeri*; 8 in *C. tupareomanaia* [Table 4]). The anteriormost pouch 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. australe*, 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 supraoccipital, 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 supraoccipital 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 (Kuitert, 2009: 93, figs. A, B). However, the female individual in the photograph was originally misidentified as the subtropical Southwest Pacific seahorse, *Hippocampus jugumus* Kuitert, 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 supraoccipital and the posterior nuchal plate); the elevated supraoccipital well separated from the cleithrum above the operculum, forming a large gap between the two areas (vs. supraoccipital 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 supraoccipital bone (vs. derived from the modified anterior nuchal); presence of dorsomedial bony crest on the posterior nuchal plate (vs. absence); cleithrum reaches mid-dorsally over anterior margins of bony dorsomedial crest (vs. ventrally on a projected horizontal line through gills in members of *Hippocampus* with the exception of *H. jugumus* [Kuitert, 2001] and the pygmy seahorse species *H. japapigu*, *H. pontohi*, *H. satomiae*, and *H. waleanus* [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. australe* 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 pipehorse 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 *Filicampus*, *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	<i>A. breviperula</i>					
2	KY066068	<i>A. tentaculata</i>	0.144				
3	MH306206	<i>C. tupareomanaia</i>	0.195	0.204			
4	MH306205	<i>I. australe</i>	0.097	0.131	0.179		
5	KY066120	<i>I. lumnitzeri</i>	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 *Ichthyology & 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 congenial 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 Waiatapu 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. australe*; Glenn Moore, Western

Australian Museum, for specimen loan of *I. australe*; 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. australe*; 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. larsonae*; 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 micro-computed tomography scans of pygmy pipehorse specimens used in this study; Richard Smith, IUCN Seahorse, Pipefish and Seadragon Specialist Group, Shane Housham and Julia Riddle, Northland Dive, and Kent Erickson, Ocean Blue Adventures, 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. australe*; 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 Brauer, Curtin University, for their gushing support of all things syngnathids and lively discussions; and Greg Misner, Aotearoa 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.

LITERATURE CITED

- Allen, G. R., D. F. Hoese, J. R. Paxton, J. E. Randall, C. Russell, W. A. Starck, F. H. Talbot, and G. P. Whitley. 1976. Annotated checklist of the fishes of Lord Howe Island. Records of the Australian Museum 30:365–454.
- Al-Jufaili, S. M., G. Hermosa, S. S. Al-Shuaily, and A. Al Mujaini. 2010. Oman fish biodiversity. Journal of King Abdulaziz University, Marine Science 21:3–51.
- Araki, M., M. Yamada, and H. Motomura. 2019. First specimen-based records of *Acentronura* (*Acentronura*) *graci-*

- lissima* (Syngnathiformes: Syngnathidae) from the Kagoshima mainland, southern Kyushu, Japan. *Nature of Kagoshima* 46:185–188. [In Japanese]
- Baker, J., H. Crawford, D. Muirhead, S. Shepherd, J. Brook, A. Brown, and C. Hall.** 2009. Uncommon, cryptic and site-associated reef fishes: results of surveys along Fleurieu Peninsula and in Encounter Bay 2009. Report for Adelaide and Mt Lofty Ranges Natural Resources Management Board, South Australia.
- Brook, F. J.** 2002. Biogeography of near-shore reef fishes in northern New Zealand. *Journal of the Royal Society of New Zealand* 322:243–274.
- Browne, R. K., J. L. Baker, and R. M. Connolly.** 2008. Syngnathids: seadragons, seahorses, and pipefishes of Gulf St Vincent, p. 162–176. *In: Natural History of Gulf St Vincent*. S. A. Shepherd, S. Bryars, I. R. Kirkegaard, P. Harbison, and J. T. Jennings (eds.). The University of Adelaide, Royal Society of South Australia Inc., Adelaide.
- Chen, C. J.** 2017. Taxonomic revision of the Syngnathinae (Pices: Syngnathidae) in Taiwan. Unpubl. master's thesis, National Sun-yat Sen University, Kaohsiung, Taiwan.
- Clark, M. R., T. Trnski, R. Constantine, J. D. Aguirre, J. Barker, E. Betty, D. A. Bowden, A. Connell, C. Duffy, S. George, S. Hannam, L. Liggins, C. Middleton, S. Mills . . . L. van Oosterom.** 2017. Biodiversity of the Kermadec Islands and offshore waters of the Kermadec Ridge: report of a coastal, marine mammal and deep-sea survey (TAN1612), New Zealand Aquatic Environment and Biodiversity Report No. 17.
- Conway, K. W., A. L. Stewart, and C. King.** 2017. A new species of the clingfish genus *Trachelochismus* from bay and estuarine areas of New Zealand (Teleostei: Gobiesocidae). *Zootaxa* 43:531–549.
- Conway, K. W., A. L. Stewart, and A. P. Summers.** 2018. A new species of sea urchin associated clingfish of the genus *Dellichthys* (Teleostei: Gobiesocidae). *ZooKeys* 740:77–95.
- Dawson, C. E.** 1980. Synopsis of the pipefishes (Syngnathidae) of New Zealand. *National Museum of New Zealand Records* 1:281–291.
- Dawson, C. E.** 1984. A new pipehorse (Syngnathidae) from Western Australia, with remarks on the subgenera of *Acentronura*. *Japanese Journal of Ichthyology* 312:156–160.
- Dawson, C. E.** 1985. Indo-Pacific Pipefishes (Red Sea to the Americas). The Gulf Coast Research Laboratory, Ocean Springs, Mississippi.
- Edgar, G., S. Stuart-Smith, R. Thomson, D. Freeman, and P. Southwood.** 2013. Reef Life Survey assessment of biodiversity in northern New Zealand marine reserves and associated coastlines. Report prepared by Aquenal Pty Ltd and Reef Life Survey Inc, Hobart, for the New Zealand Department of Conservation.
- Eme, D., M. J. Anderson, E. M. V. Myers, C. D. Roberts, and L. Liggins.** 2020. Phylogenetic measures reveal eco-evolutionary drivers of biodiversity along a depth gradient. *Ecography* 43:689–702.
- Francis, M. P.** 1979. Checklist of the marine fishes of Kaikoura, New Zealand. *Mauri ora* 7:63–71.
- Francis, M. P.** 1993. Checklist of the coastal fishes of Lord Howe, Norfolk, and Kermadec Islands, southwest Pacific Ocean. *Pacific Science* 47:136–170.
- Francis, M., and C. Duffy.** 2015. New records, checklist and biogeography of Kermadec Islands' coastal fishes. *Bulletin of the Auckland Museum* 20:481–495.
- Francis, M. P., M. A. Morrison, J. Leathwick, C. Walsh, and C. Middleton.** 2005. Predictive models of small fish presence and abundance in northern New Zealand harbours. *Estuarine, Coastal and Shelf Science* 64:419–435.
- Francis, M. P., M. A. Morrison, J. Leathwick, and C. Walsh.** 2011. Predicting patterns of richness, occurrence and abundance of small fish in New Zealand estuaries. *Marine and Freshwater Research* 62:1327–1341.
- Francis, M. P., and J. E. Randall.** 1993. Further additions to the fish faunas of Lord Howe and Norfolk Islands, southwest Pacific Ocean. *Pacific Science* 47:118–135.
- Fraser-Brunner, A., and G. P. Whitley.** 1949. A new pipefish from Queensland. *Records of the Australian Museum* 22: 148–150.
- Fricke, R., G. R. Allen, D. Amon, S. Andrefouet, W. J. Chen, J. Kinch, R. Mana, B. C. Russell, D. Tully, and W. T. White.** 2019. Checklist of the marine and estuarine fishes of New Ireland Province, Papua New Guinea, western Pacific Ocean, with 810 new records. *Zootaxa* 4588:1–360.
- Fricke, R., and M. Kulbicki.** 2006. Checklist of the shore fishes of New Caledonia. *Compendium of Marine Species from New Caledonia*:357–401.
- Fricke, R., M. Kulbicki, and L. Wantiez.** 2011. Checklist of the fishes of New Caledonia, and their distribution in the Southwest Pacific Ocean (Pisces). *Stuttgarter Beiträge zur Naturkunde A, Neue Serie* 4:341–463.
- Gomon, M. F.** 2007. A new genus and miniature species of pipehorse (Syngnathidae) from Indonesia. *Aqua* 13:25–30.
- Gordon, D. P., J. Beaumont, A. MacDiarmid, D. A. Robertson, and S. T. Ahyong.** 2010. Marine biodiversity of Aotearoa New Zealand. *PLoS ONE* 5:e10905.
- Grace, A. B.** 1976. A preliminary checklist of fishes from Great Mercury Island, north-eastern New Zealand. *Tane* 22: 103–105.
- Grace, R. V.** 1973. A checklist of fishes of the Aldermen Islands, North-Eastern New Zealand, with additions to the fishes of Red Mercury Island. *Tane* 19:13–19.
- Grandcourt, E.** 2012. Reef fish and fisheries in the Gulf, p. 127–161. *In: Coral Reefs of the Gulf*. B. M. Riegl and R. E. Dodge (eds.). Springer, Dordrecht.
- Günther, A. C. L. G.** 1870. Catalogue of the fishes in the British Museum. Volume 8. Catalogue of the Physostomi, containing the families Gymnotidae, Symbranchidae, Muraenidae, Pegasidae, and of the Lophobranchii, Plectognathi, Dipnoi, Ganoidei, Chondropterygii, Cyclostomata, Leptocardii, in the collection of the British Museum. Taylor and Francis, London.
- Hamilton, H., N. Saarman, G. Short, A. B. Sellas, B. Moore, T. Hoang, C. L. Grace, M. Gomon, K. Crow, and W. B. Simison.** 2017. Molecular phylogeny and patterns of diversification in syngnathid fishes. *Molecular Phylogenetics and Evolution* 107:388–403.
- Hardy, G. S., R. V. Grace, and M. P. Francis.** 1987. Fishes observed at the Three Kings Islands, northern New Zealand. *Records of the Auckland Institute and Museum* 18:243–250.
- Hickey, A. J., S. D. Lavery, D. A. Hannan, C. S. Baker, and K. D. Clements.** 2009. New Zealand triplefin fishes family (Tripterygiidae): contrasting population structure and mtDNA diversity within a marine species flock. *Molecular Ecology* 184:680–696.
- Housley, G. D.** 1980. Observations on the fish fauna of the Mokohinau group. *Tane* 26:83–89.

- Housley, G. D., D. J. Riddell, and R. V. Grace. 1981. A checklist of fishes from Cuvier Island, northeastern New Zealand. *Tane* 27:37–41.
- Hutchins, J. B. 2001. Checklist of fishes of Western Australia. Records of the Western Australian Museum Supplements 63:9–50.
- Johnson, J. W. 1999. Annotated checklist of the fishes of Moreton Bay, Queensland, *Memoirs of the Queensland Museum* 43:709–762.
- Jones, E., D. Parsons, M. Morrison, N. Bagley, C. Paterson, and N. Usmar. 2009. Bay of Islands OS20/20 Survey Report. Chapter 13: Fish Communities. Bay of Islands OS20/20 Survey Report 98. NIWA Taihoro Nukurangi.
- Kelly, M. 2007. A Bibliography and Literature Review for the Poor Knights Islands Marine Reserve. Department of Conservation, Northland Conservancy, Whangarei, New Zealand.
- Kingsford, M. J., D. R. Schiel, and C. N. Battershill. 1989. Distribution and abundance of fish in a rocky reef environment at the subantarctic Auckland Islands, New Zealand. *Polar Biology* 93:179–186.
- Kuiter, R. H. 2000. Seahorses, Pipefishes and Their Relatives: A Comprehensive Guide to Syngnathiformes. Twayne Publishers, Woodbridge, Connecticut.
- Kuiter, R. H. 2001. Revision of the Australian seahorses of the genus *Hippocampus* (Syngnathiformes: Syngnathidae) with descriptions of nine new species. *Records of the Australian Museum* 53:293–340.
- Kuiter, R. H. 2003. Seahorses, Pipefishes and Their Relatives. Revised. TMC Publishing, Chorleywood, UK.
- Kuiter, R. H. 2004. A new pygmy pipehorse (Pisces: Syngnathidae: *Idiotropiscis*) from eastern Australia. *Records of the Australian Museum* 562:163–165.
- Kuiter, R. H. 2009. Seahorses and Their Relatives. Aquatic Photographics, Seaford, Australia.
- Kumar, S., G. Stecher, M. Li, C. Knyaz, and K. Tamura. 2018. MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution* 35:1547–1549.
- Larson, H. K., R. S. Williams, and M. P. Hammer. 2013. An annotated checklist of the fishes of the Northern Territory, Australia. *Zootaxa* 3696:1–293.
- Leathwick, J. R., J. Elith, M. P. Francis, T. Hastie, and P. Taylor. 2006. Variation in demersal fish species richness in the oceans surrounding New Zealand: an analysis using boosted regression trees. *Marine Ecology Progress Series* 321:267–281.
- Leysen, H. 2011. Evolutionary morphology of the extremely specialized feeding apparatus in seahorses and pipefishes (Syngnathidae). Unpubl. Ph.D. diss., Ghent University, Ghent, Belgium.
- Lourie, S. A., R. A. Pollom, and S. J. Foster. 2016. A global revision of the Seahorses *Hippocampus* Rafinesque 1810 (Actinopterygii: Syngnathiformes): taxonomy and biogeography with recommendations for further research. *Zootaxa* 4146:1–66.
- McKenna, S. A. 2003. The condition of coral reefs in northwest Madagascar. A rapid marine biodiversity assessment of the coral reefs of northwest Madagascar. *Bulletin of the Rapid Assessment Program* 31:54–67.
- Morrison, M. A., M. P. Francis, and B. W. Hartill. 2002. Diurnal and tidal variation in the abundance of the fish fauna of a temperate tidal mudflat. *Estuarine, Coastal and Shelf Science* 54:793–807.
- Morrison, M. A., M. L. Lowe, C. Grant, P. J. Smith, G. Carbines, J. Reed, S. Bury, and J. Brown. 2014. Seagrass meadows as biodiversity and productivity hotspots. New Zealand Aquatic Environment and Biodiversity Report No. 137.
- Mortimer, N., H. J. Campbell, A. J. Tulloch, P. R. King, V. M. Stagpoole, R. A. Wood, M. S. Rattenbury, R. Sutherland, C. Adams, J. Collot, and M. Seton. 2017. Zealandia: Earth's hidden continent. *GSA Today* 27:27–35.
- Nakae, M., H. Motomura, K. Hagiwara, H. Senou, K. Koeda, T. Yoshida, S. Tashiro, B. Jeong, H. Hata, Y. Fukui, and K. Fujiwara. 2018. An annotated checklist of fishes of Amami-oshima Island, the Ryukyu Islands, Japan. *Memoirs of the National Museum of Nature and Science, Tokyo* 52: 205–361.
- Nicholson, J. 1979. A checklist of fishes from the Cavalli Islands, Northland, New Zealand. *Tane* 251:133–139.
- Nicholson, J., and L. I. N. Roberts. 1980. A survey of marine fishes of Urupukapuka Island, Bay of Islands, New Zealand. *Tane* 262:135–143.
- Paulin, C. D., and C. D. Roberts. 1993. Biogeography of New Zealand rockpool fishes, p. 191–199. *In: Proceedings of the 2nd International Temperate Reef Symposium*. C. N. Battershill, D. R. Schiel, G. P. Jones, R. G. Creese, and A. B. MacDiarmid (eds.). NIWA Marine, Wellington.
- Randall, J. E., and K. K. P. Lim (Eds.). 2000. A checklist of the fishes of the South China Sea. *Raffles Bulletin of Zoology, Supplement* 8:569–667.
- Rivaton, J., and B. Richer de Forges. 1990. Poissons récoltés par dragages dans le lagon de Nouvelle Calédonie. *Rapports Scientifiques et Techniques Sciences de la Mer Biologie Marine* 55:1–102.
- Roberts, C. D. 1991. Fishes of the Chatham Islands, New Zealand: a trawl survey and summary of the ichthyofauna. *New Zealand Journal of Marine and Freshwater Research* 25:1–9.
- Roberts, C. D., and A. L. Stewart. 2006. Diversity and biogeography of coastal fishes of the East Cape Region of New Zealand. *Science for Conservation* 260. Science and Technical Publishing, Department of Conservation, Wellington.
- Roberts, C. D., A. L. Stewart, and C. D. Struthers. 2015. The Fishes of New Zealand. Te Papa Press, Wellington.
- Roberts, L. I., C. Ward, and M. P. Francis. 1986. Fishes of northeastern Great Barrier Island, New Zealand. *Journal of the Royal Society of New Zealand* 16:357–62.
- Ronquist, F., S. Klopfstein, L. Vilhelmsen, S. Schulmeister, D. L. Murray, and A. P. Rasnitsyn. 2012. A total-evidence approach to dating with fossils, applied to the early radiation of the Hymenoptera. *Systematic Biology* 61: 973–999.
- Russell, B. C. 1970. A preliminary annotated checklist of fishes of the Poor Knights Islands. *Tane* 17:81–90.
- Sabaj, M. H. 2020. Codes for natural history collections in ichthyology and herpetology. *Copeia* 108:593–669.
- Short, G., R. Smith, H. Motomura, D. Harasti, and H. Hamilton. 2018. *Hippocampus japapigu*, a new species of pygmy seahorse from Japan, with a redescription of *H. pontohi* (Teleostei, Syngnathidae). *ZooKeys* 779:27–49.
- Sivaguru, K., and R. Grace. 2004. Habitat and species diversity of deep reefs and sediments at Great Barrier

- Island. Department of Conservation, Auckland Conservancy.
- Smith, J. L. B.** 1963. Fishes of the family Syngnathidae from the Red Sea and the western Indian Ocean. *Ichthyology Bulletin* 27:515–543.
- Smith, S. D. A., S. J. Dalton, and S. W. Purcell.** 2010. Distribution of Threatened and Protected species in marine habitats of the Northern Rivers region of New South Wales. A National Marine Science Centre Report to the Northern Rivers Catchment Management Authority.
- Stewart, A. L.** 2015. Family Syngnathidae: pipefishes and seahorses, p. 1050–1062. *In: The Fishes of New Zealand*. Vol. 3. C. D. Roberts, A. L. Stewart, and C. D. Struthers (eds.). Te Papa Press, Wellington.
- Temminck, C. J., and H. Schlegel.** 1850. Pisces. *In: Fauna japonica, sive, descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis, superiorum, qui summum in India Batava imperium tenent, suscepto, annis 1823–1830 collegit, notis, observationibus et adumbrationibus illustravit Ph. Fr. de Siebold. P. F. de Siebold (ed.). Lugduni Batavorum [Leiden] A. Arnz et soc.* Last part 15:270–324.
- Teske, P. R., and L. B. Beheregaray.** 2009. Evolution of seahorses' upright posture was linked to Oligocene expansion of seagrass habitats. *Biology Letters* 5:521–523.
- Trnski, T., C. A. J. Duffy, M. P. Francis, M. A. McGrouther, A. L. Stewart, C. D. Struthers, and V. Zintzen.** 2015. Recent collections of fishes at the Kermadec Islands and new records for the region. *Bulletin of the Auckland Museum* 20:463–480.
- Waite, E. R., and H. M. Hale.** 1921. Review of the lophobranchiate fishes (pipe-fishes and seahorses) of South Australia. *Records of the South Australian Museum* 1:293–324.
- Whitley, G. P.** 1948. Studies in Ichthyology No. 13. Records of the Australian Museum 22:70–94.
- Willan, R. C., J. M. Dollimore, and J. Nicholson.** 1979. A survey of fish populations at Karikari Peninsula, Northland, by scuba diving. *New Zealand Journal of Marine and Freshwater Research* 13:447–458.
- Willis, T. J.** 1995. A preliminary description of the fish fauna of Taranga (Hen) Island, North-Eastern New Zealand. *Tane* 35:57–68.
- WoRMS Editorial Board.** 2021. World Register of Marine Species. Available from <https://www.marinespecies.org> at VLIZ. Accessed 2021-02-01. doi: 10.14284/170.

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

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