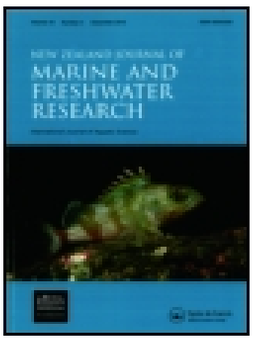

New Zealand Journal of Marine and Freshwater Research

ISSN: 0028-8330 (Print) 1175-8805 (Online) Journal homepage: http://www.tandfonline.com/loi/tnzm20

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To cite this article: Peter J. Smith , Robin P. McPhee & Clive D. Roberts (2006) DNA and meristic evidence for two species of giant stargazer (Teleostei: Uranoscopidae: Kathetostoma) in New Zealand waters, New Zealand Journal of Marine and Freshwater Research, 40:3, 379-387, DOI: 10.1080/00288330.2006.9517429

To link to this article: http://dx.doi.org/10.1080/00288330.2006.9517429

New Zealand Journal of Marine and Freshwater Research, 2006, Vol. 40: 379–387
0028–8330/06/4003–0379

DNA and meristic evidence for two species of giant stargazer (Teleostei: Uranoscopidae: *Kathetostoma*) in New Zealand waters

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Abstract The taxonomic status of the banded giant stargazer in New Zealand waters is uncertain. Mitochondrial DNA partial sequences of the cytochrome *b* gene and the control region, along with three meristic characters (numbers of dorsal fin rays, anal fin rays, and vertebrae), were compared among six recognised species of *Kathetostoma* and specimens of the banded giant morph. New Zealand specimens referred to as banded giant stargazer were shown to be a discrete species distinguished from the giant stargazer *K. giganteum* from New Zealand and the banded *K. laeve* and *K. canaster* from Australia, by cytochrome *b* and control region sequences and meristic counts. This undescribed species occurs over a wide geographic range from the Snares shelf (48°S) to the Norfolk Ridge (32°S) in the Tasman Sea, and is largely sympatric with *K. giganteum*. The two New Zealand species occupy different depth ranges, with the banded giant stargazer generally occurring in shallower water (<320 m) than *K. giganteum* (12–1000 m).

M05054; online publication date 7 July 2006
Received 19 August 2005; accepted 13 December 2005

Keywords mitochondrial DNA; meristics; stargazer; *Kathetostoma*; taxonomy; species discrimination; undescribed species

INTRODUCTION

The armour-head stargazers (Uranoscopidae) are small to medium size fish widely distributed in temperate and tropical oceans and seas (Pietsch 1989). All species are bottom dwelling "ambush predators", capable of burying beneath sandy substrates, and are characterised by a heavily armoured and flattened head with dorsally directed eyes (Pietsch 1989). Seven genera are recognised globally, with four species in four genera found in New Zealand waters (Pietsch 1989): the spotted stargazer *Genyagnus monopterygius* (Forster & Schneider, 1801) is widespread in coastal waters; the brown stargazer *Xenocephalus armatus* Kaup, 1858 (junior synonym *Gnathagnus innotablis* Waite, 1904) is found in coastal waters in northern New Zealand; the deepwater scaly stargazer *Pleuroscopus pseudodorsalis* Barnard, 1927 is occasionally reported from water >600 m; and the giant stargazer *Kathetostoma giganteum* Haast, 1873 is widespread around New Zealand but more common around the South Island in coastal and deep water (<1000 m) (Anderson et al. 1998).

Stargazers are taken as by-catch in domestic trawl fisheries around the South Island and as by-catch in deep water (700–1000 m) trawl fisheries on the Chatham Rise to the east and the Snares shelf to the south of New Zealand (Sullivan et al. 2005). The commercial catch of stargazers has increased over the past 25 years from <1000 to >3000 t per annum, with c. 70% taken from the west and south coasts of the South Island. The current total allowable catch (TAC) is set at 5117 t (Sullivan et al. 2005). The stargazer catch is not recorded to the species level but includes *Genyagnus monopterygius* and *Xenocephalus armatus* with the majority of the catch thought to be *Kathetostoma* (Sullivan et al. 2005).

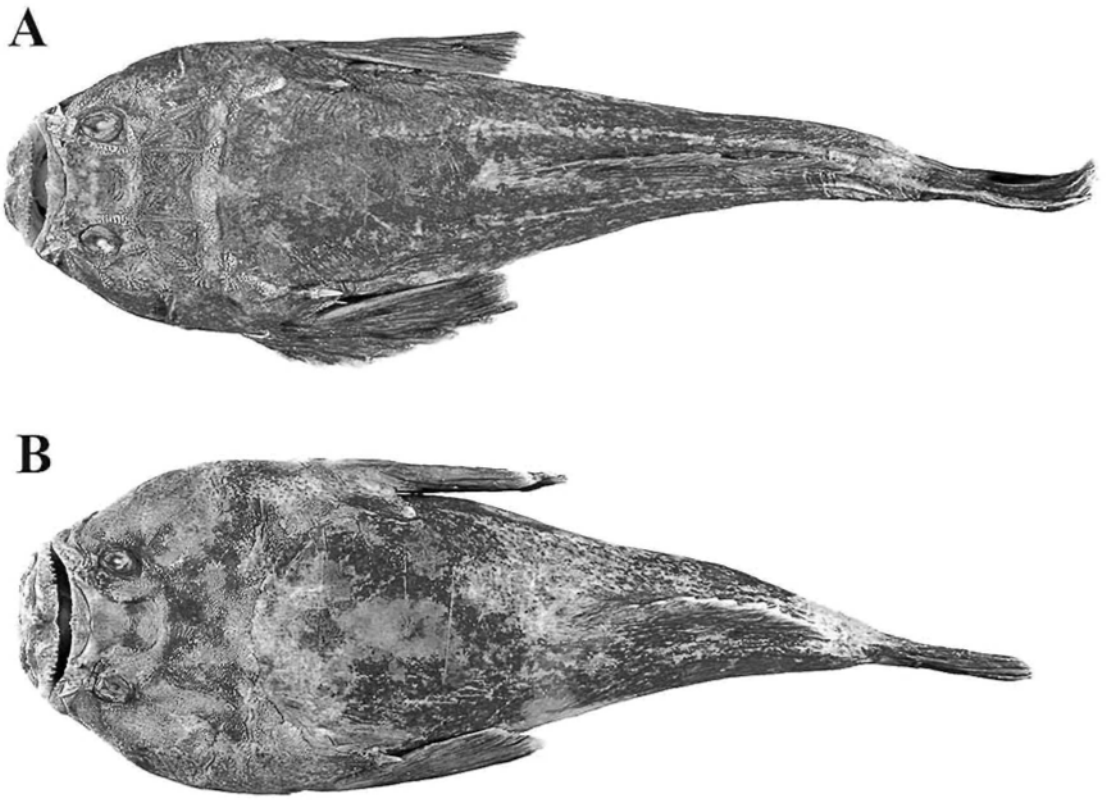

Fig. 1 Two species of New Zealand giant stargazers. **A**, Giant stargazer *Kathetostoma giganteum*, NMNZ P.41571, 370 mm SL, Chatham Rise. **B**, Banded giant stargazer *Kathetostoma* sp., NMNZ P.41505, 340 mm SL, Snares Shelf (note relatively wide head and body, and two diffuse dark bands crossing the body between the pectoral fins and below the dorsal fin).

In the genus *Kathetostoma* Günther, 1860, seven species are currently recognised (Berry & Anderson 1961; Pietsch 1989; Gomon 1994; Gomon et al. 1994); three species occur around Australia: the speckled stargazer *K. canister* Goman & Last, 1987 the deepwater stargazer *K. nigrofasciatum* Waite & McCulloch, 1915, and the common stargazer *K. laeve* (Bloch & Schneider, 1801); two species occur in the western central North Atlantic: *K. albigutta* Bean, 1892 and *K. cubana* Barbour, 1941; one species *K. averruncus* Jordan & Bollman, 1890 in the tropical eastern Pacific; and one species, the giant stargazer *K. giganteum* is endemic to New Zealand waters (Pietsch 1989).

Fishery and museum scientists have reported an undescribed species or morph of *Kathetostoma* from commercial catches around southern New Zealand (Paul 1986); listed as *Kathetostoma* sp. (Roberts et al. in press). This species or morph is generally recognised by the presence of two broad vertical bands across the dorsal and lateral surface of the body and the caudal fin (Fig. 1), and is variously recorded as: the banded stargazer *Kathetostoma* sp. (Paul 1986); the Australian brown stargazer *K. laevis* (Hatanaka et al. 1989); *K. laeve* (Amaoka et al. 1996); the banded stargazer (Hurst & Bagley 1994); and the banded giant stargazer *Kathetostoma* sp. (Anderson et al. 1998). Australian specimens of *K. laeve* are also characterised by broad dark bands across the dorsal and lateral surfaces (Last et al. 1983), as are specimens of the more recently described *K. canaster* (Gomon & Last 1987). There is further confusion over the identity of the New Zealand banded form, because specimens exhibit a range of banding patterns from weak banding on a light greenish body colour to masked bands on a

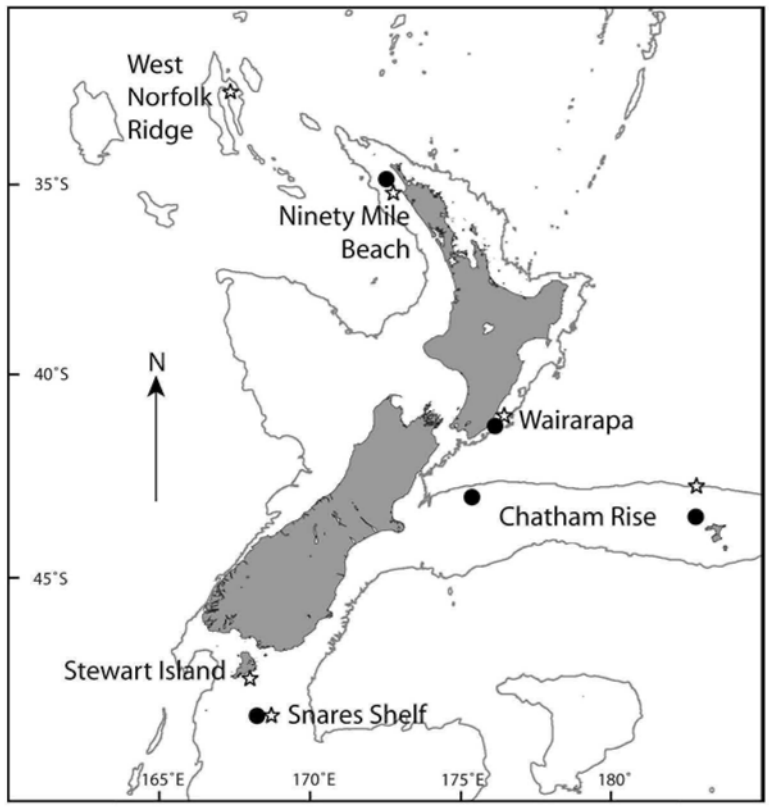

Fig. 2 Distribution of *Kathetostoma* specimens collected around New Zealand. Thin line represents the 1000 m contour. (● *Kathetostoma giganteum*; ★ Banded giant stargazer.)

dark brown body colour (R. P. McPhee pers. obs.). In addition, some specimens recorded as *K. giganteum* appear to be banded. For example, a photograph of a giant stargazer taken in shallow water off the northeast coast of New Zealand and identified as *K. giganteum* (Doak 1979) appears to be the banded form.

DNA based techniques are increasingly used to resolve taxonomic relationships of closely related fish species, particularly for taxa exhibiting a range of colour morphs (Bernardi et al. 2002; Kai et al. 2002). Here we use mitochondrial DNA sequences and meristic counts, to compare *Kathetostoma* specimens and tissue samples from Australasia and North America, to resolve the taxonomic status of the banded giant stargazer in New Zealand waters.

MATERIALS AND METHODS

Specimens of *Kathetostoma* were collected by research and commercial trawl around New Zealand between 1995 and 2004 (Fig. 2). Whole specimens were chilled or frozen and returned to the laboratory, where they were registered in the National Fish Collection at the Museum of New Zealand Te Papa Tongarewa (NMNZ) (Table 1) and the specimens dissected on the right side to remove a small piece of muscle tissue. Tissue samples were sealed in individual plastic bags and stored at –70°C. Whole specimens were fixed in 10% formalin and preserved in 50% isopropanol. Institutional acronyms followed standard abbreviations (Leviton et al. 1985); TS is the tissue sample number.

Specimens recorded as giant stargazer *K. giganteum* were collected on the eastern Chatham Rise (n = 3), 43°44′S, 177°43′W, depth 230–288 m; NMNZ P.34884 (TS242), P.34907 (TS252), P.41583 (TS524); the western Chatham Rise (n = 3), 43°04′S, 175°36′E, 330–360 m, NMNZ P.41571 (TS515), P.41576 (TS516), P.41579 (TS637); on the Snares Shelf (n = 3) 48°14′S, 168°23′E, 345–350 m, NMNZ P.41584 (TS632), P.41585 (TS633), P.41569 (TS637); off the Wairarapa coast (n = 3), 41°15′S, 176°05′E, 90–150 m, NMNZ P.42091 (TS569), P.42081 (TS570), P.42135 (TS571); and off Ninety Mile Beach (n = 3), 35°42′S, 173°37′E, c. 100 m, NMNZ P.40880 (TS694), P.40883 (TS697), P.40885 (TS699).

Specimens recorded as the banded giant stargazer *Kathetostoma* sp., were collected on the eastern Chatham Rise (n = 5), 43°26′S, 177°27′W, depth 230–327 m, NMNZ P.34913 (2) (TS260, 261), P.41581 (TS522), P.41733 (TS529), P.42084 (TS547); around Stewart Island (n = 2), 47°30′S, 168°E, 180–240 m; NMNZ P.42132 (TS559), P.42133 (TS567); off the Wairarapa coast (n = 3), 41°5′S, 176°05′E, 90–150 m, specimens not retained; on the Snares Shelf (n = 3, 48°14′S, 168°23′E, 345–350 m, NMNZ P.41509 (TS628), P.41511 (631), P.41510 (TS630); off Ninety Mile Beach (n = 5), 35°42′S, 173°37′E, c. 100 m, NMNZ P.42144 (TS676), P.42152 (TS683), P.42153 (2) (TS684, 685), P.42142 (TS687); and on the West Norfolk Ridge (n = 3), 32°40′S, 167°35′E, 116–360 m, NMV A25157–003 (2) (TS1193, 1194), AMS I.42757–004 (TS1195).

In addition, muscle tissue samples were available from one specimen of *K. nigrofasciatum* (NMV A24527) from Victoria, Australia; two specimens of *K. laeve* (AMS I.43540–001, AMS I.43541–001) from New South Wales, Australia; two specimens of *K. canaster* from New South Wales (NMV A23546, NMNZ P.41791), and two from Tasmania (NMNZ P.41789, NMNZ P.41790), Australia; two specimens of *K. albigutta* (KU 27026, KU 29676) from the mid Atlantic Bight and the Gulf of Mexico, respectively; and two specimens of *K. averruncus* (KU 28145, KU 28152) from southern California. Two species were used as outgroups to root the phylogenetic trees: the brown stargazer *Xenocephalus armatus* (NMNZ P.42089, TS565) collected in Cook Strait (41°29′S 175°00′E) and the scaly stargazer *Pleuroscopus pseudodorsalis* (not retained) collected on the Three Kings Rise (33°40′S 173°02′E).

Meristics

Counts of three characters, the numbers of rays in the dorsal and anal fins and number of vertebrae, were made on whole preserved specimens registered in the NMNZ collection (list available from authors). Vertebral counts, including the hypural plate, were taken from radiographs. Comparable meristic data for *K. canaster*, *K. nigrofasciatum*, *K. laeve*, *K. albigutta*, *K. cubana*, and *K. averruncus* were taken from the literature (see Table 1).

Mitochondrial DNA

Total genomic DNA was extracted from 200–500 mg of muscle tissue by homogenisation and digestion with proteinase-K at 55°C for 4 h. After digestion DNA was extracted with phenol:chloroform, followed by chloroform:isoamyl alcohol, and precipitated with 70% ethanol at –20°C, after Taggart et al. (1992). The DNA pellet was air dried and resuspended in 40 μl sterile water and stored at –20°C.

Two regions of the mitochondrial genome were amplified by the polymerase chain reaction (PCR) in 50 μl volumes in a Cetus DNA thermocycler (Perkin-Elmer Corporation, Connecticut). The primer pair Cyb 2 and tGludg (Palumbi et al. 1991), that amplify an approximate 400 base pair region of the cytochrome *b* gene in fish (Baker et al. 1995), and the primer pair L-15995 and H-16498 (Meyer et al. 1994), that amplify an approximate 400 base pair region of the control region, were used with all tissue samples. Amplifications for cytochrome *b* were carried out using an initial denaturation of 94°C for 2 min; 34 cycles of 92°C for 60 s, 54°C for 60 s, and 72°C for 90 s, followed by an extension at 72°C for 8 min, and for the control

Table 1 Selected meristic characters in eight *Kathetostoma* species. (No., number of specimens examined for counts; ND, no data available; Vertebrae, total number of vertebrae including the hypural plate.)

Species	No.	Dorsal rays	Anal rays	Vertebrae	Source
K. averruncus	15–19	13–16	13–15	28–30	(Jordan & Evermann 1898; Fierstine & Werner 1963; Watson 1996)
K. cubana	11	13–15	13–14	25–29	(Berry & Anderson 1961; Pietsch 1989)
K. albigutta	23	13–15	12–15	25–29	(Berry & Anderson 1961; Pietsch 1989)
K. nigrofasciatum	ND	13–15	13–14	27–29	(Gomon & Last 1987; Gomon 1994)
K. laeve	ND	16–17	13–15	28–30	(Gomon & Last 1987; Gomon 1994)
K. canaster	17	16–18	15–16	31–33	(Gomon & Last 1987; Gomon 1994)
K. giganteum	39	17–20	17–19	33–35	this paper
Banded giant	15	14–15	14–15	29–30	this paper

region using an initial denaturation of 94°C for 2 min; 35 cycles of 94°C for 60 s, 54°C for 60 s, and 72°C for 120 s, followed by an extension at 72°C for 7 min. DNA samples were purified using the QIAquick gel extraction kit (Qiagen). Sequences were determined using the ABI Taq DyeDeoxy™ Terminator Cycle Sequencing Kit according to the manufacturers directions (Applied Biosystems Inc.) and run on an ABI prism autosequencer.

Sequence alignment and data analysis

Sequences were edited in CHROMAS 2.3 (Technelysium, Queensland, Australia), and aligned in the BIOEDIT 5.0.9 program (Hall 1999). Phylogenetic analyses were performed separately for the cytochrome *b* and control region sequences. The control region is non-coding and subject to different evolutionary constraints from the cytochrome *b* gene. Phylogenetic congruence of the two data sets was tested with a partition homogeneity test (Farris et al. 1994). Five hundred partition replicates were analysed under maximum parsimony using heuristic searches in PAUP version 4.0 (Swofford 2000).

Phylogenies were explored with neighbour-joining (NJ) and maximum likelihood (ML) methods using MEGA version 2.1 (Kumar et al. 2001) and PAUP version 4.0 (Swofford 2000). Modeltest version 3.06 (Posada & Crandall 1998) was used to determine the best-fit model using likelihood ratio tests: the HKY + G model incorporating gamma distribution rates (Hasegawa et al. 1985) for cytochrome *b* and the TrN + I model with unequal base frequencies (Tamura & Nei 1993) for control region sequences. Gaps in the control region sequences were treated as missing data. Support for each internode was evaluated by bootstrap replications (Felsenstein 1985) with 1000 pseudoreplicates for NJ, and 200 for ML trees. Bayesian phylogenetic trees were estimated with MrBayes version 3.0 (Huelsenbeck & Ronquist 2001) for the cytochrome *b* and control region sequences, using the substitution models established above. Four simultaneous Monte Carlo chains were run for 1×10^6 generations, saving the current tree every 100 generations. A consensus tree with posterior probabilities was created with a burn-in value equal to 5000 (the first 5000 trees were discarded). *Xenocephalus armatus* and *Pleuroscopus pseudodorsalis* were used to root the cytochrome *b* trees, but were not used with the control region sequences owing to the lack of alignment with the *Kathetostoma* sequences over a highly variable mid region c. 110 base pairs. Net sequence divergence between haplotypes was estimated with Kimura's two parameter model (Kimura 1981), so that data were comparable with published cytochrome *b* sequence divergences in fishes (Johns & Avise 1998).

Conformance of data to a molecular clock was tested with a log-likelihood ratio test (Felsenstein 1981), using the best-fit model with and without the molecular clock restriction, and n–2 d.f., where n = the number of taxa. Sequences were deposited in the GenBank nucleotide sequence database under the accession numbers DQ165248–282 (control region sequences) and DQ165283–317 (cytochrome *b* sequences).

RESULTS

Meristics

Counts for three meristic characters are presented in Table 1. All three characters, numbers of dorsal fin rays, anal fin rays, and vertebrae, distinguish *K. giganteum* and the banded giant stargazer from New Zealand with no overlap. Dorsal fin ray counts also distinguish the New Zealand banded giant stargazer from Australian specimens of *K. laeve* and *K. canaster* with no overlap observed. The number of anal fin rays overlap between the New Zealand banded giant stargazer and *K. canaster*, *K. laeve*, and *K. nigrofasciatum*, whereas the number of vertebrae overlap between the New Zealand banded giant stargazer and *K. laeve* and *K. nigrofasciatum*.

Phylogenetic relationships

Partition homogeneity tests rejected phylogenetic congruence ($P = 0.006$), justifying separate analyses of the cytochrome *b* and control region sequence data sets. Unambiguously aligned sequences were obtained for the cytochrome *b* and control region in 46 specimens. For the *Kathetostoma* cytochrome *b* sequences there were 391 bases, of which 91 were both variable and phylogenetically informative. Twelve of the nucleotide substitutions resulted in an amino acid change. For the control region sequences there were 371 bases of which 154 were variable and 146 phylogenetically informative. The mid region, c. 160 base pairs, was highly variable with small (1–6 bp) insertions and deletions, as expected for the non-coding control region, with a faster rate of evolution than cytochrome *b* (Meyer 1994).

NJ and ML trees for cytochrome *b* produced well-resolved and similar topologies with evidence for strongly supported clades among the recognised *Kathetostoma* species, which form a monophyletic group (Fig. 3). The Bayesian analysis generated a

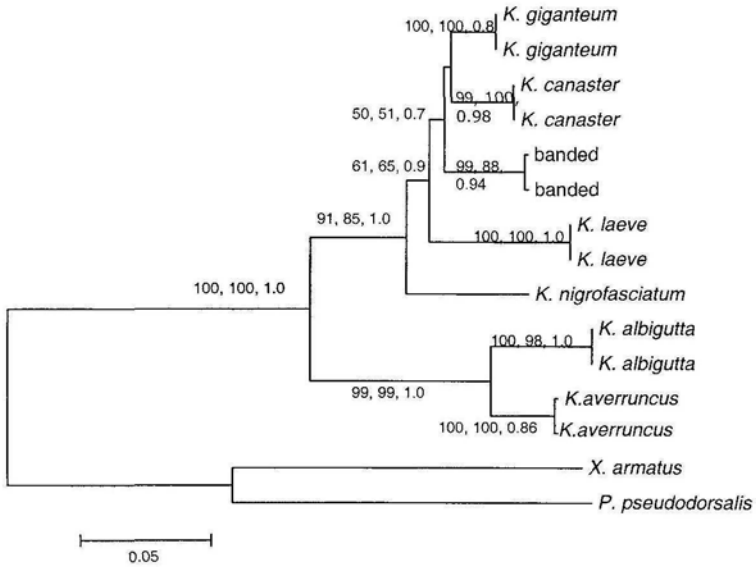

Fig. 3 Phylogenetic relationships of *Kathetostoma* samples based on partial cytochrome *b* gene sequences. Scale bar represents an interval of Hasegawa et al.'s (1985) genetic distance. Numbers at nodes are bootstrap percentages (>50%), based on distance and maximum likelihood, and Bayesian inference posterior probability values (>0.8). Neighbour-joining tree has been rooted with the uranoscopids *Pleuroscopus pseudodorsalis* and *Xenocephalus armatus*.

similar topology. The banded giant stargazer from New Zealand is clearly differentiated from the New Zealand *K. giganteum* and the banded *K. laeve* and *K. canaster* from Australia, with high bootstrap support and 1.0 posterior probability. NJ and ML trees for the control region sequences produced well-resolved and similar topologies with evidence for strongly supported clades among the recognised *Kathetostoma* species (Fig. 4). The Bayesian analysis generated a similar topology. The banded giant stargazer from New Zealand is clearly differentiated from the New Zealand *K. giganteum* and the banded *K. laeve* and *K. canaster* from Australia, with high bootstrap support and 1.0 posterior probability.

Net sequence divergence among the Australasian species, excluding the banded giant stargazer from New Zealand, ranged from 0.041 to 0.111 for cytochrome *b* and 0.118–0.328 for the control region; and was 0.063 and 0.076, respectively, between the two American species *K. albigutta* and *K. averruncus* (Table 2). The banded giant stargazer had a similar net divergence among the Australasian species, cytochrome *b* 0.053–0.094 and control region 0.146–0.255 (Table 2). *Kathetostoma giganteum* from New Zealand and *K. canaster* from Australia showed lower net sequence divergences than *K. giganteum* and the banded giant stargazer from New Zealand, for both cytochrome *b* and control regions sequences (Table 2).

The molecular clock hypothesis was rejected with likelihood-ratio tests, indicating a mutational rate heterogeneity among clades (cytochrome *b* $\chi^2 = 64$, $P < 0.001$, d.f. = 10; control region $\chi^2 = 192$, $P < 0.001$, d.f. = 17), and consequently the nucleotide sequence divergences could not be used to estimate the time of phylogenetic events.

DISCUSSION

The cytochrome *b* gene has been the most frequently sequenced mtDNA region in fish and interspecific sequence divergences exhibit a wide range of values from 0.01 to 0.25 (Johns & Avise 1998). The maximum cytochrome *b* divergences between pairs of sister species of fish ranged from 0.02 to 0.08 (McCune & Lovejoy 1998) and from 0.00 to 0.06 among intraspecific populations, the higher intraspecific population values being mostly freshwater species and a transatlantic marine species (McCune & Lovejoy 1998). Divergence among sympatric species was generally lower than among allopatric species (McCune & Lovejoy 1998). The net cytochrome *b* sequence divergence among the Australasian species of *Kathetostoma* ranged from 0.04 to 0.11, and was 0.06 between the two American species separated by the Panama Isthmus (Table 2). The New Zealand banded giant stargazer showed a similar net divergence of 0.05 to 0.09 among the Australasian species. Control region sequence divergence was greater among the *Kathetostoma* species, ranging from 0.12 to 0.33

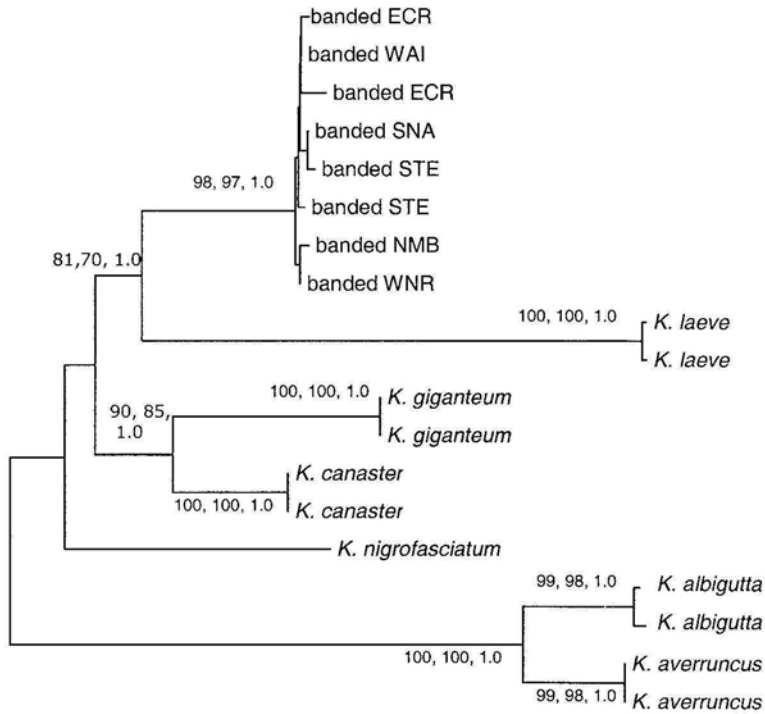

Fig. 4 Phylogenetic relationships of *Kathetostoma* samples based on partial control region sequences. Scale bar represents an interval of Tamura & Nei's (1993) genetic distance, for an unrooted neighbour-joining tree. Numbers at nodes are bootstrap percentages (>70%), based on distance, maximum likelihood, and Bayesian inference posterior probability values (>0.8). (ECR, Eastern Chatham Rise; NMB, Ninety Mile Beach; SNA, Snares Shelf; STE, Stewart Island; WAI, Wairarapa coast; WNR, West Norfolk Ridge.)

Table 2 Net sequence divergence for mtDNA cytochrome *b* (above diagonal) and control region (below diagonal) between species of *Kathetostoma*; within taxon sequence divergences along diagonal (cytochrome *b*/control region) shown in bold.

	giganteum	n. sp	*canaster*	*laeve*	*nigrofasciatum*	*albigutta*	*averruncus*
K. giganteum	**0/0**	0.053	0.041	0.076	0.086	0.194	0.178
Banded giant	0.193	**0.007/0.007**	0.057	0.094	0.088	0.193	0.156
K. canaster	0.118	0.146	**0/0**	0.086	0.089	0.184	0.167
K. laeve	0.341	0.255	0.313	**0/0.003**	0.111	0.193	0.191
K. nigrofasciatum	0.217	0.193	0.191	0.328	**0/0**	0.194	0.180
K. albigutta	0.395	0.375	0.397	0.607	0.400	**0/0.006**	0.063
K. averruncus	0.409	0.380	0.394	0.542	0.374	0.076	**0.003/0**

among Australasian species, as expected for this faster evolving region (Donaldson & Wilson 1999), and was 0.07 between the two American species. The New Zealand banded giant stargazer showed a similar net divergence of 0.14 to 0.26 among the Australasian species.

The mtDNA, coupled with the meristic data, are interpreted as providing strong evidence for a second species of *Kathetostoma* in New Zealand waters. This second species is not the banded *K. laeve*, nor *K. canaster* from Australia, as reported by previous authors, but is new to science. The new species of *Kathetostoma* appears to be endemic to New Zealand, but a formal description of the species awaits a revision of the genus (M.F. Gomon pers. comm.). DNA markers are clearly useful in determining species relationships, although the different phylogenetic trees revealed with cytochrome *b* and control region sequences (note the relative relationships of *K. nigrofasciatum*, *K. laeve*, and *K. canaster* in Fig. 3 and 4) indicate that additional coding sequences of DNA should be considered. The non-coding control region sequences were characterised by variable indels in the mid region.

The distribution of the new banded giant stargazer is wider than suggested from current trawl-fishery records, which note the banded giant stargazer occurring only around the south of the South Island (47–48°S), with an isolated record from the northwest Chatham Islands (c. 43°S) (Anderson et al. 1998). Specimens of the new banded giant stargazer for the present study were identified from the Snares Shelf (48° S), on the eastern Chatham Rise (178° W), off the west coast of the North Island (43° S), and in the northern Tasman Sea (32° S). The spatial distribution shows considerable overlap with *K. giganteum*, which has been reported between 34 and 51°S (Anderson et al. 1998). However the two species differ in depth distributions, with the banded giant stargazer generally found in shallower water, 76–315m, than *K. giganteum*, 12–1082m (Anderson et al. 1998), although new records for the Wanganella Bank on the west Norfolk Ridge found the banded giant stargazer to depths of 325–497m (unpublished NORFANZ fishes database). The different depth distributions suggest that the two species of giant stargazer occupy different ecological niches, and may therefore be taken as by-catch in different trawl fisheries. The banded giant stargazer is probably more common in coastal domestic trawl fisheries, whereas *K. giganteum* might be caught by both coastal and deepwater trawl fisheries and be subject to different fishing pressures. Ideally, the two species would be distinguished and recorded separately, allowing monitoring and management of each species, rather than under the current single species.

ACKNOWLEDGMENTS

We thank Peter McMillan (NIWA) for constructive comments on the manuscript. We are grateful to Margaret McVeagh (NIWA) for laboratory assistance and Andrew Stewart and Carl Struthers (Te Papa) for help with tissue sampling and specimen management. Stargazers were collected in New Zealand by Neil Bagley, Martin Cryer, and Dean Stotter (NIWA), Juri Guskov and Julian Hall (MFish Scientific Observer Programme), Vaughan Wilkinson and Jorge Hurt (Simunovich Fisheries, Auckland), George Imlach (FV *Rowallan*, Wellington) , and Alan Dunford (FV *Marlene II*, Stewart Island); in Australia by Martin Gomon (NMV), Al Graham (CSIRO), and Ken Graham (NSW State Fisheries); and on the Wanganella Bank by staff on the NORFANZ voyage (RV *Tangaroa*). Tissue samples of related species were supplied by Di Bray (NMV), Mark McGrouther and Tom Trinsky (AMS), and Andrew Bentley (University of Kansas). Fig. 1 was produced by Carl Struthers (Te Papa). The research was funded by the New Zealand Foundation for Research, Science and Technology (contract MNZ0203), Biosystematics of New Zealand EEZ Fishes project.

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