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Wei-Jen Chen, Hsuan-Ching Ho, Philippe Borsa. Taiwanese records of oblong large-eye seabream *Gymnocranius oblongus* (Teleostei: Lethrinidae) and other rare or undetermined large-eye seabreams . *Frontiers in Marine Science*, Frontiers Media, 2016, 3, pp.107. 10.3389/fmars.2016.00107. ird-01331954

HAL Id: ird-01331954

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Submitted on 15 Jun 2016

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To be cited as: Chen W-J, Ho H-C, Borsa P (2016) Taiwanese records of oblong large-eye seabream *Gymnocranius oblongus* (Teleostei: Lethrinidae) and other rare or undetermined large-eye seabreams. *Frontiers in Marine Science* 3, 107. doi: 10.3389/fmars.2016.00107

Taiwanese records of oblong large-eye seabream *Gymnocranius oblongus* (Teleostei: Lethrinidae) and other rare or undetermined large-eye seabreams

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Running title: New records of rare large-eye seabreams

The oblong large-eye seabream *Gymnocranius oblongus* Borsa, Béarez and Chen, 2010, has been described based on specimens from New Caledonia, the only locality where this species has been recorded up to now. Here, new records are reported from Taiwan, which is located over 7,000 km from the previously known site of occurrence. Nucleotide sequences at the *cytochrome b* locus of the Taiwanese samples of *G. oblongus* were provided and compared to those of the conspecific New Caledonian samples. The results showed little intraspecific DNA variation among the sequences (only three segregating sites along the 1140 bp long aligned sequences). Further population genetic analysis revealed a relatively high level of genetic differentiation ($\Phi_{ST} = 0.286$) indicating limited gene flow between the two populations. The records thus available suggest a wide and antitropical distribution for this relatively rare and poorly known species. In addition to this finding, we report the first Taiwanese records of *Gymnocranius satoi* Borsa, Béarez, Paijo and Chen 2013, and of two undetermined *Gymnocranius* specimens that potentially represent two new species.

Keywords: Fishes, new record, new species, distribution, Taiwan, New Caledonia, diversity

INTRODUCTION

Large-eye seabreams (Monotaxinae) comprise medium- to large-sized benthic fishes occurring over sandy or rubble substrates at or in the vicinity of coral reefs, at depths ranging from 1 to 180 meters (Carpenter and Allen, 1989). Large-eye seabreams regularly occur at local fish markets throughout the tropical Indo-West Pacific (Carpenter and Allen, 1989; authors' personal observations). Despite the importance of several large-eye seabream species for human consumption, our knowledge on their biology, taxonomy and biogeography is still limited. Currently, 13 species belonging to four genera are recognized in this fish group that is classified as one of two subfamilies of the perciform fish family Lethrinidae (Carpenter and Allen, 1989; Borsa et al., 2010, 2013). *Gymnocranius* is the most speciose genus, with 10 species described thus far. The oblong large-eye seabream, *Gymnocranius oblongus* Borsa, Béarez and Chen 2010 is one of the three species that have been described since the synopsis of Carpenter and Allen (1989); the other two are *Gymnocranius satoi* Borsa, Béarez, Paijo and Chen, 2013 and *Gymnocranius superciliosus* Borsa, Béarez, Paijo and Chen, 2013. The specimens used for the description of *G. oblongus* had all been collected from New Caledonia; its distribution was thought to be limited to the Coral Sea (Borsa et al., 2010). This fish is characterized by an oblong, fusiform body, a slightly rounded snout, an elongate tail with rounded tips and sub-horizontal, wavy blue lines or dashes on snout and cheeks (Borsa et al., 2010). It is distinct from *Gymnocranius grandoculis* (Valenciennes, 1830), regularly found at fish markets (e.g., in Taiwan), by a more slender body which is also more symmetrical dorso-ventrally and by a more elongated caudal fin. Another remarkable feature of *G. oblongus* is its prominent forehead, though less conspicuously so than its relative *Gymnocranius microdon* (Bleeker, 1851).

Two specimens purchased from local fish markets in Taiwan were identified as *G. oblongus*. The main purpose of the present work is to put the newly discovered Taiwanese specimens of this species on record. Cytochrome *b*-gene sequences obtained from the Taiwanese specimens were compared to those from New Caledonia to evaluate the infra-specific genetic diversity and to estimate the level of genetic differentiation between the two populations. Additional records of rare or undetermined *Gymnocranius* from Taiwan are also provided in this paper.

MATERIALS AND METHODS

We examined 81 large-eye seabream *Gymnocranius* specimens collected between 2011 and 2015 at several local fish markets in the eastern and southern parts of Taiwan and on Little Liuqiu and Penghu Islands in the Taiwan Strait (see supplementary Table S1). The two specimens of *G. oblongus*, which had been caught by line, were purchased from fish sellers, one by HCH in Hengchun town, southern Taiwan on 05 August 2011, and the other one by WJC in Magong, Penghu Islands (Taiwan Strait) on 03 May 2015. The specimens were photographed shortly after collection. Standard length (SL), body depth at origin of first dorsal fin (BD), head length, snout length, eye diameter, inter-orbital width and other parameters were measured to the nearest millimeter. Species identification followed Borsa et al. (2010). Other monotaxine specimens collected by us in Taiwanese waters were identified using diagnostic morphological traits, as provided in the relevant literature (Carpenter and Allen, 1989; Borsa et al., 2013; Nakabo, 2013) and/or assessed against the genetic library that we are currently building for the Lethrinidae.

Small pieces of muscle-tissue were excised from the specimens, preserved in 95% ethanol, and stored at -20°C in the Marine Biodiversity and Phylogenomics laboratory at Institute of Oceanography, National Taiwan University (NTU), Taipei with tissue identification numbers LET439 and LET1209, respectively. The Hengchun specimen was lost afterwards. The Penghu specimen was preserved in formaldehyde and deposited at the ichthyological collection of the NTU Museums, Taipei under registration no. NTUM-10819. In total, we accessed tissue samples from seven *G. oblongus* specimens including the two specimens from Taiwan and five specimens previously collected from New Caledonia (including the holotype and all

three paratypes of the species), one *G. satoi* specimen, and two unidentified *Gymnocranius* specimens from Taiwan (Table 1). Genomic DNA was extracted using an automated DNA-extractor (LabTurbo 48 Compact System with LGD 480-220 kits: Taigene Bioscience Corporation, Taipei) following the manufacturer's protocol. Protocols for cytochrome *b* gene amplification and sequencing have been outlined in Borsa et al. (2013). The sequences were deposited in GenBank (<http://www.ncbi.nlm.nih.gov/>) as a genetic reference for future DNA-identification and research on large-eye seabreams.

The sequences were aligned with homologous sequences from *Gymnocranius elongatus* Senta, 1973, *G. grandoculis*, and *Gymnocranius griseus* (Temminck and Schlegel, 1843) published by Lo Galbo et al. (2002) and retrieved from GenBank (accession nos. AF381260, AF381275, and AF381259, respectively), and those of *G. superciliosus* (from New Caledonia) and *G. satoi* (from West Papua) that have been produced previously (Borsa et al., 2013).

The softwares PopART (University of Otago, available from <http://popart.otago.ac.nz>) and PAUP* (Swofford, 2002) were used to compute the number of haplotypes, the minimum spanning network, pairwise *p* distances, nucleotide diversity, and segregating (polymorphic) sites to assess the intra- and inter-specific genetic diversity of the *cytochrome b* sequences. The level of genetic differentiation between populations was estimated by ϕ_{ST} , Excoffier et al.'s (1992) estimator of Wright's (1951) F_{ST} , the standardized among-population variance in allele frequency using ARLEQUIN v. 3.5 (Excoffier and Lischer, 2010). The nucleotide-substitution model chosen was TN93, the best model according to the Bayesian information criterion (MEGA6; Tamura et al., 2013) among the suite of models implemented in ARLEQUIN v. 3.5.

Estimates of genetic differentiation in *G. oblongus* were compared to those between populations of shore fishes from the Coral Sea and the northern South China Sea or adjacent locations. In blacktip grouper *Epinephelus fasciatus* and largescale mullet *Planiliza* sp. H (one of 10 cryptic species in the genus *Planiliza*; Durand et al., 2015), genetic differences were estimated between populations from the Coral Sea or from nearby Fiji and the northern South China Sea and Philippines or nearby Ryukyu Islands, Japan, based on the nucleotide sequence data compiled or produced by, respectively, Borsa et al. (2016) and Durand et al. (2012). For all other species examined, F_{ST} values or equivalents were taken directly from the relevant literature.

RESULTS AND DISCUSSION

The photographs of the two oblong large-eye seabream specimens from Taiwan are shown in Fig. 1. The measurements on the single specimen kept as voucher (NTUM-10819) were the following: SL 241 mm, BD 95 mm, head length 68 mm, snout length 28 mm, eye diameter 21 mm, and inter-orbital width 29 mm; the count of pored scales on lateral line was 48. The ratio of SL to BD was 2.6, which was at the lower end of the range reported for six specimens from New Caledonia (2.6 – 2.8) (Borsa et al., 2010). The SL/BD ratio in the Hungchen specimen (Fig. 1A) was around 2.5. The combination of three features diagnose adult specimens of *G. oblongus* relative to all other species described to date in the genus *Gymnocranius*, namely, *G. audleyi* Ogilby, 1916, *G. elongatus*, *G. euanus* (Günther, 1879), *G. frenatus* Bleeker, 1873, *G. grandoculis*, *G. griseus*, *G. microdon* (Bleeker, 1851), *G. satoi* and *G. superciliosus* (Carpenter and Allen, 1989; Borsa et al., 2010, 2013). These are: (1) “sub-horizontal, wavy blue lines or dashes on snout and cheeks”; (2) “fusiform body”; and (3) “elongate tail” (Borsa et al., 2010: 245). The sub-horizontal wavy blue lines on snout were observed in the larger of our two Taiwanese specimens (Fig. 1b), but not in the smaller specimen (Fig. 1a). Both specimens had a fusiform body with remarkable dorso-ventral symmetry (Fig. 1). Both possessed an elongate tail (Fig. 1).

Juvenile and pre-adult *Gymnocranius* spp. usually present several transversal dark bars on body sides (Carpenter and Allen, 1989). One of these dark bars runs from around the base of the second soft ray of

the dorsal fin to the base of the anal fin spines (Carpenter and Allen, 1989). The equivalent transversal dark bar in the smaller *G. oblongus* specimen from Taiwan (indicated by an arrow on Fig. 1a) ran forward and crossed with another transversal dark bar running from the base of 5th to 6th dorsal spin to ventral part of body at approximately the place of the tip of the pectoral fin tip; a faint dark blotch was visible at the crossing position (Fig. 1a). These pigmentation patterns also characterize an early juvenile specimen from New Caledonia (Borsa et al., 2010: figure 3).

Seven new cytochrome *b* gene sequences of *G. oblongus* (GenBank nos. KU597058-KU597064) being produced in this study resulted in three haplotypes. The nucleotide diversity was 0.18%. Individual LET 439 from Taiwan possessed the same haplotype as 4/5 individuals from New Caledonia. The haplotype represented by the Penghu specimen (LET1209) diverged by two mutation steps from it. Three segregating sites were observed along the 1140 bp-long aligned sequences of *G. oblongus*. A total of 323 variable nucleotide sites was observed among all included sequences of *Gymnocranius* spp. The average interspecific nucleotide divergence (estimated from pairwise uncorrected *p*-distances) was 11.02% whereas the average infra-specific nucleotide divergence was 0.08% in *G. oblongus* and 0.4% in *G. satoi* (see below).

The estimate of genetic differentiation (Φ_{ST}) between the New Caledonian and Taiwanese populations of *G. oblongus* was 0.286 ($P = 0.057$; permutation test; ARLEQUIN) suggesting limited gene flow. This was the fourth-ranking value in Table 2. The three species with higher F_{ST} were *E. fasciatus*, the coral trout *Plectropomus leopardus* and the narrow-barred Spanish mackerel *Scomberomorus commerson*. The high value in *E. fasciatus* reflects the occurrence of a divergent mitochondrial lineage within a sample (Borsa et al., 2016). The high value in *P. leopardus* is caused by the occurrence of two mitochondrial clades with allopatric distribution (van Herwerden et al., 2009). The high values reported for *S. commerson* stem from differences between multiple divergent mitochondrial clades (Fauvelot and Borsa, 2011). The phylogeographic structure uncovered in all three cases suggests the occurrence of cryptic species. Homologous estimates of genetic differentiation in all other species listed in Table 2 were < 0.200 . The high Φ_{ST} value observed here for *G. oblongus* suggests geographically isolated populations, hence an antitropical distribution.

Among the other Monotaxinae collected from Taiwan, four specimens were identified as *G. satoi* and 15 others could only be identified to the genus *Gymnocranius* based on the available morphological keys. These *Gymnocranius* specimens can be classified into two different morphological types based on their transversal dark bar patterns on body sides and fin ray colors (yellowish or reddish) (Fig. 2; Fig. 3). They also showed substantial genetic divergence (*p*-distance $> 10.7\%$) with all other known species in the genus for which cytochrome *b* sequence data were available, indicating potential new species. These two species have been mentioned for the first time by Borsa et al. (2013) as *Gymnocranius* sp. D (Fig. 2) and *Gymnocranius* sp. E (Fig. 3). *Gymnocranius satoi* is the red-finned "*Gymnocranius* sp." depicted previously (Sato 1986; Carpenter and Allen 1989; Nakabo, 2013) and formally described in Borsa et al. (2013). Its distribution includes New Caledonia, Japan and Raja Ampat in West Papua, and possibly the Great Barrier Reef, the Solomon Sea, the Bismarck Sea, the Pacific coast of New Guinea and the Lesser Sunda Islands (Borsa et al., 2013, and references therein). The present record from Taiwan is new.

CONCLUDING REMARKS

The oblong large-eye seabream likely has an antitropical distribution in the western Pacific. Thus, most monotaxine species, now including *G. oblongus*, have a relatively wide distribution in the Indo-West Pacific (Carpenter and Allen 1989; Borsa et al., 2013; this study). The new records and species reported in this study make up to ten known and two undescribed monotaxine species in Taiwanese waters (Shao 2016; this study).

ACKNOWLEDGMENTS

We would like to thank WJC's lab members, especially Pei-Chun Lo, for assistance in the laboratory, and Hsiu-Chen Lin and Jhen-Nien Chen, for the management of specimens. This work was supported by research grants from the Ministry of Science and Technology, Taiwan (MOST 101-2611-M-002-016-MY3 and MOST 104-2611-M-002-002-MY3 to WJC).

AUTHORS' CONTRIBUTIONS

WJC and PB contributed to the conception and design of the work, analyzed and interpreted the data, and wrote the paper; WJC and HCH collected and managed the samples; HCH provided precious photographs taken from the fresh fish specimens. WJC collected the molecular data and led the project including the search of funding support for completing this study.

CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found online at:
<http://journal.frontiersin.org/article/10.3389/fmars.2016.00107>

REFERENCES

- Bleeker, P. (1851). Nieuwe bijdrage tot de kennis der ichthyologische fauna van Celebes. *Nat. Tijdschr. Ned.-Indië* 2, 209–224.
- Bleeker, P. (1873). Mededeelingen omtrent eene herziening der Indisch-archipelagische soorten van *Epinephelus*, *Lutjanus*, *Dentex* en verwante geslachten. *Verslag. Mededeel. Koninkl. Akad. Wetenschappen Afdel. Natuurk. Ser. 2* 7, 40–46.
- Borsa, P., Béarez, P., and Chen, W.-J. (2010). *Gymnocranius oblongus* (Teleostei: Lethrinidae), a new large-eye bream species from New Caledonia. *C. R. Biol.* 333, 241–247. doi: 10.1016/j.crv.2009.12.015
- Borsa, P., Béarez, P., Paijo, S., and Chen, W.-J. (2013). *Gymnocranius superciliosus* and *Gymnocranius satoi*, two new large-eye breams (Sparoidea: Lethrinidae) from the Coral Sea and adjacent regions. *C. R. Biol.* 336, 233–240. doi: 10.1016/j.crv.2013.06.003
- Borsa, P., Durand, J.-D., Chen, W.-J., Hubert, N., Muths, D., Mou-Tham, G., and Kulbicki, M. (2016). Comparative phylogeography of the western Indian Ocean reef fauna. *Acta Oecol.* 72, 72–86. doi:10.1016/j.actao.2015.10.009
- Carpenter, K.E., and Allen, G.R. (1989). FAO species catalogue, vol.9, Emperor fishes and large-eye breams of the world (family Lethrinidae), an annotated and illustrated catalogue of lethrinid species known to date. *FAO Species Synopsis* 125, 1–118.
- Craig, M.T., Eble, J.A., Bowen, B.W., and Robertson, D.R. (2007). High genetic connectivity across the Indian and Pacific Oceans in the reef fish *Myripristis berndti* (Holocentridae). *Mar. Ecol. Prog. Ser.* 334, 245–254.
- Durand, J.-D., and Borsa, P. (2015). Mitochondrial phylogeny of grey mullets (Acanthopterygii: Mugilidae) suggests high proportion of cryptic species. *C. R. Biol.* 338, 266–277.

- Durand, J.-D., Shen, K.-N., Chen, W.-J., Jamandre, B.-W., Blel, H., Diop, K., Nirchio, M., Garcia de Leon, F.J., Whitfield, A.K., Chang, C.-W., and Borsa, P. (2012). Systematics of the grey mullets (Teleostei: Mugiliformes: Mugilidae): Molecular phylogenetic evidence challenges two centuries of morphology-based taxonomy. *Mol. Phyl. Evol.* 64, 73-92.
- Excoffier, L., Smouse, P.E., and Quattro, J.M. (1992). Analysis of molecular variance inferred from metric distances among DNA haplotypes - application to human mitochondrial-DNA restriction data. *Genetics* 131, 479–491.
- Excoffier, L., and Lischer, H.E. (2010). Arlequin suite ver. 3.5: a new series of programs to perform population genetics analyses under Linux and Windows. *Mol. Ecol. Resour.* 10, 564–567. doi: 10.1111/j.1755-0998.2010.02847.x.
- Fauvelot, C., and Borsa, P. (2011). Patterns of genetic isolation in narrow-barred Spanish mackerel (*Scomberomorus commerson*) across the Indo-West Pacific. *Biol. J. Linn. Soc.* 104, 886-902. doi: 10.1111/j.1095-8312.2011.01754.x
- Fitzpatrick, J.M., Carlon, D.B., Lippe, C., and Robertson, D.R. (2011). The West Pacific diversity hotspot as a source or sink for new species? Population genetic insights from the Indo-Pacific parrotfish *Scarus rubroviolaceus*. *Mol. Ecol.* 20, 219-234. doi: 10.1111/j.1365-294X.2010.04942.x
- Gaither, M.R., Bowen, B.W., Bordenave, T.R., Rocha, L.A., Newman, S.J., Gomez, J.A., van Herwerden, L., and Craig, M.T. (2011). Phylogeography of the reef fish *Cephalopholis argus* (Epinephelidae) indicates Pleistocene isolation across the Indo-Pacific Barrier with contemporary overlap in the Coral Triangle. *BMC Evol. Biol.* 11, 189.
- Günther, A. (1879) Notice of two new species of fishes from the South seas. *Ann. Mag. Nat. Hist. Ser. 5* 4, 136–137.
- Horne, J.B., and van Herwerden, L. (2013). Long-term panmixia in a cosmopolitan Indo-Pacific coral reef fish and a nebulous genetic boundary with its broadly sympatric sister species. *J. Evol. Biol.* 26, 783-799.
- Horne, J.B., van Herwerden, L., Choat, J.H., and Robertson, D.R. (2008). High population connectivity across the Indo-Pacific: Congruent lack of phylogeographic structure in three reef fish congeners. *Mol. Phyl. Evol.* 49, 629-638.
- Liu, S.-Y.V., Chang, F.-T., Borsa, P., Chen, W.-J., and Dai, C.-F. (2014). Phylogeography of the humbug damselfish, *Dascyllus aruanus* (Linnaeus, 1758): evidence of Indo-Pacific vicariance and genetic differentiation of peripheral populations. *Biol. J. Linn. Soc.* 113, 931-942.
- Lo Galbo, A., Carpenter, K.E., and Reed, D.L. (2002). Evolution of trophic types in emperor snappers (*Lethrinus*, Lethrinidae, Percoidae) based on cytochrome *b* gene sequence variation. *J. Mol. Evol.* 54, 754–762.
- Nakabo, T. (ed.) (2013) *Fishes of Japan with pictorial keys to the species, third edition*. Tokyo: Tokai University Press, 2428 p.
- Ogilby, J.D. (1916). Edible fishes of Queensland. Parts IV through IX. *Mem. Queensland Mus.* 5, 127–177, pls. 14–23.
- Planes, S., and Fauvelot, C. (2002). Isolation by distance and vicariance drive genetic structure of a coral reef fish in the Pacific Ocean. *Evolution* 56, 378-399.
- Sato, T. (1986). “A systematic review of the sparoid fishes of the subfamily Monotaxinae,” in *Indo-Pacific fish biology: proceedings of the second international conference on Indo-Pacific fishes*, eds., T. Uyeno, R. Arai, T. Taniuchi, and K. Matsuura (Tokyo: Ichthyol. Soc. Japan), 602–612.
- Shao, K.T. (2016). Taiwan Fish Database. WWW Web electronic publication. <http://fishdb.sinica.edu.tw>, (2016-1-30).
- Senta, T. (1973). A new sparoid fish, *Gymnocranius elongatus* from the southern South China Sea. *Japan. J. Ichthyol.* 20, 135–144.

- Swofford, D.L. (2002). PAUP*. *Phylogenetic analysis using parsimony (*and other methods)*. Version 4. Sunderland MA: Sinauer Associates.
- Tamura, K., Stecher, G., Peterson, D., FilipSKI, A., and Kumar, S. (2013). MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Mol. Biol. Evol.* 30, 2725–2729. doi: 10.1093/molbev/mst197
- Temminck, C.J., and Schlegel, H. (1843). “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 1823-30 collegit, notis observationibus et adumbrationibus. Parts 2-4* eds. P.F. von. Siebold, C.J. Temminck, and W. de Haan. (Lugduni, Batavorum), 21-72.
- Valenciennes, A. (1830). “Livre sixième, partie I, Des Sparoïdes” in *Histoire naturelle des poissons, tome sixième*, eds. G. Cuvier, and A. Valenciennes (Paris: F.G. Levrault, Paris), 141–163
- van Herwerden, L., Choat, J.H., Newman, S.J., Leray, M., and Hillersøy, G. (2009). Complex patterns of population structure and recruitment of *Plectropomus leopardus* (Pisces: Epinephelidae) in the Indo-West Pacific: implications for fisheries management. *Mar. Biol.* 156, 1595-1607.
- Winters, K.L., van Herwerden, L., Choat, J.H., and Robertson, D.R. (2010). Phylogeography of the Indo-Pacific parrotfish *Scarus psittacus*: isolation generates distinctive peripheral populations in two oceans. *Mar. Biol.* 157, 1679-1691.
- Wright, S. (1951). The genetical structure of populations. *Ann. Eugen.* 15, 323-354.

Figure legends

Fig. 1 *Gymnocranius oblongus* from Taiwanese waters. (a) Specimen from Hengchun, southern Taiwan, collected on 15 August 2011; standard length ~150 mm (photographed by HCH); *arrow* indicates oblique dark bar; (b) Specimen no. NTUM10819 from Penghu Islands, Taiwan Strait, collected on 03 May 2015; standard length 244 mm (photographed by WJC).

Fig. 2 *Gymnocranius* sp. D from Taiwanese waters. Specimen from Hengchun, southern Taiwan, collected on 19 August 2011; standard length 148 mm (photographed by HCH).

Fig. 3 *Gymnocranius* sp. E from Taiwanese waters. Specimen no. NMMBA-21547 from Hengchun, southern Taiwan, collected on 19 August 2011; standard length 183 mm (photographed by HCH).

Table 1 List of *Gymnocranius* specimens referred to in text, with sampling details, collection nos. and GenBank accession nos. *IRDN*, Institut de recherche pour le développement, Nouméa; *MBPL*, Marine Biodiversity and Phylogenomics Laboratory, Taipei; *MNHN*, Museum national d'histoire naturelle, Paris; *NTUM*, National Taiwan University museums, Taipei; *NMMBA*, National Museum of Marine Biology and Aquarium, Pingtung, Taiwan

Species, Collection site	Collection date	Field no.	Collection no.	MBPL no.	GenBank no.	Remark
<i>G. oblongus</i>						
Nouméa fish market	12 Jan. 2005	IRDN z199	MNHN 2009-0007	LET12	KU597059	paratype
Nouméa fish market	01 Apr. 2006	IRDN 20060401	MNHN 2009-0008	LET5	KU597058	paratype
Pointe Maa, New Caledonia	31 May 2008	IRDN 20080531B	MNHN 2009-0009	LET90	KU597061	holotype
SW lagoon, New Caledonia	22 Nov. 2008	IRDN 20081122	MNHN 2009-0005	LET51	KU597060	paratype
Nouvelle, New Caledonia	10 April 2009	IRDN 20090410A	-	LET963	KU597063	-
Hengchun, S. Taiwan	15 Aug. 2011	20110815 HC006	-	LET439	KU597062	-
Penghu, Taiwan Strait	03 May 2015	Penghu050315-93	NTUM 10819	LET1209	KU597064	voucher
<i>G. satoi</i>						
Little Liuqiu, Taiwan Strait	14Sept. 2013	-	NTUM10760	LET992	KX357715	voucher
<i>Gymnocranius</i> sp. D						
Hengchun, S. Taiwan	19 Aug. 2011	20110819HC006	-	LET427	KX357714	-
<i>Gymnocranius</i> sp. E						
Hengchun, S. Taiwan	19 Aug. 2011	20110819HC004	NMMBA21546	LET426	KX357713	voucher

Table 2 Estimates of genetic differentiation (F_{ST} or equivalent) between populations of shore fishes from the Coral Sea and the northern South China Sea (SCS) (or adjacent location). NC New Caledonia; GBR Great Barrier Reef

Species	Marker	Range	F_{ST}	Reference
<i>Acanthurus triostegus</i>	5 allozymes	NC-Batanga	0.065	Planes and Fauvelot (2002)
<i>Cephalopholis argus</i>	<i>cytochrome b</i>	GBR-Palawan	0.070	Gaither et al. (2011)
<i>Cephalopholis argus</i>	Multi-locus nuclear	GBR-Palawan	0.128	Gaither et al. (2011)
<i>Dasyllus aruanus</i>	<i>cytochrome b</i>	6955-7528 km	0.060-0.117	Liu et al. (2014)
<i>Dasyllus aruanus</i>	7 microsatellites	6955-7528 km	0.019-0.028	Liu et al. (2014)
<i>Epinephelus fasciatus</i>	<i>CO1</i>	GBR-SCS/Philippines	0.307	Borsa et al. (2016)
<i>Gymnocranius oblongus</i>	<i>cytochrome b</i>	~7000 km	0.286	Present study
<i>Myripristis berndti</i>	<i>cytochrome b</i>	Lizard-Okinawa	-0.105	Craig et al. (2007)
<i>Naso hexacanthus</i>	mtDNA control region	GBR-Philippines	0.029	Horne and van Herwerden (2013)
<i>Naso hexacanthus</i>	<i>CO1</i>	GBR-Philippines	0.083	Horne and van Herwerden (2013)
<i>Naso hexacanthus</i>	<i>Eno1N</i> (nuclear)	GBR-Philippines	0.026	Horne and van Herwerden (2013)
<i>Naso hexacanthus</i>	<i>CK</i> (nuclear)	GBR-Philippines	-0.034	Horne and van Herwerden (2013)
<i>Naso vlamingii</i>	mtDNA control region	GBR-Philippines	-0.004	Horne et al. (2008)
<i>Planiliza</i> sp. H	<i>cytochrome b</i>	NC/Fiji-Taiwan/Japan	-0.028	Durand and Borsa (2015)
<i>Planiliza</i> sp. H	<i>CO1</i>	NC/Fiji-Taiwan/Japan	0.013	Durand and Borsa (2015)
<i>Plectropomus leopardus</i>	mtDNA control region	~7000 km	0.885	van Herwerden et al. (2009)
<i>Scarus psittacus</i>	mtDNA control region	GBR - Taiwan	0.021	Winters et al. (2010)
<i>Scarus rubroviolaceus</i>	9-15 microsatellites	GBR - Taiwan	0.010-0.020	Fitzpatrick et al. (2011)
<i>Scomberomorus commerson</i>	mtDNA control region	~7000 km	0.332-0.675	Fauvelot and Borsa (2011)



Fig. 2 - Chen et al.



20110819HL 056
百 鱒 5 148mm SL

Fig. 3 - Chen et al.



2011081946004
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Supplementary Table 1. List of 81 Taiwanese *Gymnocranius* spp. samples collected during the present survey

Sample ID	Genus	Species	Locality	Field no.	Voucher no.
LET82	<i>Gnatbodentex</i>	<i>aureolineatus</i>	Taitung, Taiwan	ASIZP0801861	-
LET436	<i>Gnatbodentex</i>	<i>aureolineatus</i>	Hengchun, Taiwan	20110803 HC006	NMMBP13833
LET437	<i>Gnatbodentex</i>	<i>aureolineatus</i>	Hengchun, Taiwan	20110815 HC004	-
LET438	<i>Gnatbodentex</i>	<i>aureolineatus</i>	Hengchun, Taiwan	20110815 HC005	-
LET987	<i>Gymnocranius</i>	<i>elongatus</i>	Fugang, Taitung, Taiwan	-	NTUM10758
LET1165	<i>Gymnocranius</i>	<i>elongatus</i>	Fugang, Taitung, Taiwan	-	NTUM10807
LET1166	<i>Gymnocranius</i>	<i>elongatus</i>	Fugang, Taitung, Taiwan	-	NTUM10807
LET1167	<i>Gymnocranius</i>	<i>elongatus</i>	Fugang, Taitung, Taiwan	-	NTUM10807
LET1024	<i>Gymnocranius</i>	<i>elongatus</i>	Hengchun, Taiwan	-	NTUM10773
LET1025	<i>Gymnocranius</i>	<i>elongatus</i>	Hengchun, Taiwan	-	NTUM10773
LET585	<i>Gymnocranius</i>	<i>elongatus</i>	Kenting, Taiwan	-	-
LET893	<i>Gymnocranius</i>	<i>elongatus</i>	Kenting, Taiwan	-	NTUM10742
LET901	<i>Gymnocranius</i>	<i>elongatus</i>	Kenting, Taiwan	-	NTUM10742
LET763	<i>Gymnocranius</i>	<i>elongatus</i>	Penghu, Taiwan	-	NTUM10726
LET724	<i>Gymnocranius</i>	<i>elongatus</i>	Taitung, Taiwan	B4	-
LET726	<i>Gymnocranius</i>	<i>elongatus</i>	Taitung, Taiwan	-	NTUM10720
LET250	<i>Gymnocranius</i>	<i>elongatus</i>	Kenting, Taiwan	-	NTUM10701
LET1002	<i>Gymnocranius</i>	<i>grandoculis</i>	Fugang Taitung, Taiwan	-	NTUM10767
LET1003	<i>Gymnocranius</i>	<i>grandoculis</i>	Fugang Taitung, Taiwan	-	NTUM10767
LET1169	<i>Gymnocranius</i>	<i>grandoculis</i>	Fugang Taitung, Taiwan	-	NTUM10809
LET1170	<i>Gymnocranius</i>	<i>grandoculis</i>	Fugang Taitung, Taiwan	-	NTUM10809
LET1171	<i>Gymnocranius</i>	<i>grandoculis</i>	Fugang Taitung, Taiwan	-	NTUM10809
LET1172	<i>Gymnocranius</i>	<i>grandoculis</i>	Fugang Taitung, Taiwan	-	NTUM10809
LET1173	<i>Gymnocranius</i>	<i>grandoculis</i>	Fugang Taitung, Taiwan	-	NTUM10809
LET1174	<i>Gymnocranius</i>	<i>grandoculis</i>	Fugang Taitung, Taiwan	-	NTUM10809
LET1175	<i>Gymnocranius</i>	<i>grandoculis</i>	Fugang Taitung, Taiwan	-	NTUM10809
LET1176	<i>Gymnocranius</i>	<i>grandoculis</i>	Fugang Taitung, Taiwan	-	NTUM10809
LET1177	<i>Gymnocranius</i>	<i>grandoculis</i>	Fugang Taitung, Taiwan	-	NTUM10809
LET1178	<i>Gymnocranius</i>	<i>grandoculis</i>	Fugang Taitung, Taiwan	-	NTUM10809
LET889	<i>Gymnocranius</i>	<i>grandoculis</i>	Hengchun Taiwan	-	NTUM10740
LET547	<i>Gymnocranius</i>	<i>grandoculis</i>	Hengchun, Taiwan	-	NTUM10713
LET1140	<i>Gymnocranius</i>	<i>grandoculis</i>	Hengchun, Taiwan	-	NTUM10800
LET1013	<i>Gymnocranius</i>	<i>grandoculis</i>	Jialeshuei, Taiwan	20110722佳樂水02	NMMB13837
LET607	<i>Gymnocranius</i>	<i>grandoculis</i>	Kenting, Taiwan	-	-
LET902	<i>Gymnocranius</i>	<i>grandoculis</i>	Kenting, Taiwan	-	NTUM10746
LET1011	<i>Gymnocranius</i>	<i>grandoculis</i>	Kenting, Taiwan	20110919HBH001	NMMBP14071
LET83	<i>Gymnocranius</i>	<i>grandoculis</i>	Little Liuqiu, Taiwan	ASIZP0804375	-
LET989	<i>Gymnocranius</i>	<i>grandoculis</i>	Little Liuqiu, Taiwan	-	NTUM10765
LET990	<i>Gymnocranius</i>	<i>grandoculis</i>	Little Liuqiu, Taiwan	-	NTUM10765
LET997	<i>Gymnocranius</i>	<i>grandoculis</i>	Little Liuqiu, Taiwan	-	NTUM10765
LET1210	<i>Gymnocranius</i>	<i>grandoculis</i>	Penghu, Taiwan	Penghu050415-1	NTUM10817
LET723	<i>Gymnocranius</i>	<i>grandoculis</i>	Taitung, Taiwan	B3	-
LET425	<i>Gymnocranius</i>	<i>grandoculis</i>	Hengchun, Taiwan	20110819 HC005	-
LET1000	<i>Gymnocranius</i>	<i>griseus</i>	Fugang, Taitung, Taiwan	-	NTUM10768
LET1001	<i>Gymnocranius</i>	<i>griseus</i>	Fugang, Taitung, Taiwan	-	NTUM10768
LET1007	<i>Gymnocranius</i>	<i>griseus</i>	Fugang, Taitung, Taiwan	-	NTUM10768
LET1008	<i>Gymnocranius</i>	<i>griseus</i>	Fugang, Taitung, Taiwan	-	NTUM10768
LET1009	<i>Gymnocranius</i>	<i>griseus</i>	Fugang, Taitung, Taiwan	-	NTUM10768
LET1010	<i>Gymnocranius</i>	<i>griseus</i>	Fugang, Taitung, Taiwan	-	NTUM10768
LET1168	<i>Gymnocranius</i>	<i>griseus</i>	Fugang, Taitung, Taiwan	-	NTUM10808
LET722	<i>Gymnocranius</i>	<i>griseus</i>	Taitung, Taiwan	B2	-
LET734	<i>Gymnocranius</i>	<i>griseus</i>	Taitung, Taiwan	-	NTUM10722
LET988	<i>Gymnocranius</i>	<i>microdon</i>	Fugang, Taitung, Taiwan	-	NTUM10759
LET1026	<i>Gymnocranius</i>	<i>microdon</i>	Hengchun, Taiwan	-	NTUM10772
LET1023	<i>Gymnocranius</i>	<i>microdon</i>	Hengchun, Taiwan	-	NTUM10772
LET1027	<i>Gymnocranius</i>	<i>microdon</i>	Hengchun, Taiwan	-	NTUM10772
LET1145	<i>Gymnocranius</i>	<i>microdon</i>	Hengchun, Taiwan	-	NTUM10804
LET251	<i>Gymnocranius</i>	<i>microdon</i>	Kenting, Taiwan	-	NTUM10702
LET1209	<i>Gymnocranius</i>	<i>oblongus</i>	Penghu, Taiwan	Penghu050315-93	NTUM10819
LET439	<i>Gymnocranius</i>	<i>oblongus</i>	Hengchun, Taiwan	20110815 HC006	-
LET1361	<i>Gymnocranius</i>	<i>satoi</i>	Hengchun, Taiwan	-	NTUM10834
LET1012	<i>Gymnocranius</i>	<i>satoi</i>	Kenting, Taiwan	20110919HBH002	NMMBP21547
LET992	<i>Gymnocranius</i>	<i>satoi</i>	Little Liuqiu, Taiwan	-	NTUM10760
LET1014	<i>Gymnocranius</i>	<i>satoi</i>	Hengchun, Taiwan	20110513HC002	NMMB12114
LET1191	<i>Gymnocranius</i>	sp. D	Hengchun, Taiwan	-	NTUM10826

LET1362	<i>Gymnocranius</i>	sp. D	Hengchun, Taiwan	-	NTUM10835
LET1363	<i>Gymnocranius</i>	sp. D	Hengchun, Taiwan	-	NTUM10835
LET1211	<i>Gymnocranius</i>	sp. D	Penghu, Taiwan	Penghu050415-2	NTUM10818
LET427	<i>Gymnocranius</i>	sp. D	Hengchun, Taiwan	20110819HC006	-
LET998	<i>Gymnocranius</i>	sp. E	Fugang Taitung, Taiwan	-	NTUM10766
LET999	<i>Gymnocranius</i>	sp. E	Fugang Taitung, Taiwan	-	NTUM10766
LET1004	<i>Gymnocranius</i>	sp. E	Fugang Taitung, Taiwan	-	NTUM10766
LET1005	<i>Gymnocranius</i>	sp. E	Fugang Taitung, Taiwan	-	NTUM10766
LET1006	<i>Gymnocranius</i>	sp. E	Fugang Taitung, Taiwan	-	NTUM10766
LET890	<i>Gymnocranius</i>	sp. E	Hengchun Taiwan	-	NTUM10741
LET891	<i>Gymnocranius</i>	sp. E	Hengchun Taiwan	-	NTUM10741
LET892	<i>Gymnocranius</i>	sp. E	Hengchun Taiwan	-	NTUM10741
LET1192	<i>Gymnocranius</i>	sp. E	Hengchun, Taiwan	-	NTUM10827
LET426	<i>Gymnocranius</i>	sp. E	Hengchun Taiwan	20110819HC004	NMMBP21546
LET1360	<i>Monotaxis</i>	<i>grandoculis</i>	Hengchun, Taiwan	-	NTUM10833
LET1384	<i>Monotaxis</i>	<i>grandoculis</i>	Little Liuqiu, Taiwan	-	-