

**A REVIEW AND MOLECULAR PHYLOGENY OF THE MORAY EEL  
SUBFAMILY UROPTERYGIINAE (ANGUILLIFORMES: MURAENIDAE)  
FROM TAIWAN, WITH DESCRIPTION OF A NEW SPECIES**

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**ABSTRACT.** – The following eight muraenid species of the subfamily Uropterygiinae are recognized from Taiwan: *Anarchias allardicei* Jordan & Starks, *Channomuraena vittata* (Richardson), *Cirrimaxilla formosa* Chen & Shao, *Scuticaria tigrina* (Lesson), *S. marmorata* (Lacepède), *Uropterygius macrocephalus* (Bleeker), *U. micropterus* (Bleeker), and *U. oligospondylus*, new species, described from three specimens, one each from Taiwan, Solomon Islands and Vanuatu. This new moray eel is distinguished from its sibling species, *U. macrocephalus*, by the following features: greater body depth at gill opening 7.3 (vs. 4.6% of total length); fewer vertebrae 100–103 (vs. 109–115); and grey body background with blackish reticular pattern (vs. black to blackish-brown body background with brown snowflake pattern). Phylogenetic relationships of seven species were examined using nucleotide sequence data from the 1,842 bp fragment of the complete mitochondrial ND5 gene. Morphological features and mitogenetic affinities strongly suggest that the so-called “*Uropterygius*” *marmoratus* should be placed in *Scuticaria* rather than in *Uropterygius*. The genetic analysis suggests that *U. oligospondylus* is distinct from the other two species of *Uropterygius* in Taiwan. The results also suggest that the employment of ND5 gene sequences is rather useful for identification of species and for obtaining reasonable insights into the phylogeny of the subfamily Uropterygiinae muraenid species.

**KEY WORDS.** – moray eel, taxonomy, new species, molecular phylogeny, ND5.

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## INTRODUCTION

The subfamily Uropterygiinae (sensu Nelson, 2006) comprises the following four genera: *Anarchias*, *Channomuraena*, *Scuticaria* and *Uropterygius*, which together include about 36 muraenid species found around the world. Reviews and descriptions of new species in the genus *Anarchias* and *Uropterygius* in Australia, New Zealand, Japan, Indo-Pacific and central Pacific have been provided by Böhlke & McCosker (1982, 2001), Gosline (1958), Hatooka (1984), McCosker et al. (1984), McCosker & Smith (1997) and Randall & Golani (1995). The basic classification of the genera was laid down by Chen et al. (1997). Chen & Shao (1995) added a new genus, *Cirrimaxilla*, and described the type species, *Cirrimaxilla formosa*.

Chen et al. (1994) reviewed the muraenid eels from Taiwan, and recorded four species belonging to two genera of subfamily Uropterygiinae. Chen et al. (1997) recorded six species belonging to five genera of Uropterygiinae. During 2006–2007 in a series of projects entitled “Diversity, molecular phylogeny and reproductive ecology of the Anguilliformes fishes of Taiwan and the Western Pacific”, we collected many specimens of moray eels from the waters around Taiwan. Among these collections, it was noticed that there was an exceptional specimen which had similar head profile but distinct different pattern from *Uropterygius macrocephalus* (Bleeker, 1864). After examining this specimen and comparing its morphology and molecular characteristics with other similar moray species, we propose and describe it here as a new species, *Uropterygius oligospondylus* H. M. Chen, J. E. Randall & K. H. Loh.

Phylogenetic studies of muraenid fishes have commonly been based on morphometric, vertebral counting methods; mitochondrial DNA sequences have seldom been analysed. According to the literature (Inoue et al., 2001, 2003), only *Gymnothorax kidako* has been studied with respect to mitochondrial DNA and basal actinopterygian relationships. A comprehensive taxonomic review of Uropterygiinae moray eels revealed that there were no studies on the molecular phylogeny of the NADH dehydrogenase ND5 gene. This gene has been shown to be informative in phylogenetic analysis of fishes (Miya & Nishida, 2000; Ikejima et al., 2004; Chiang & Chen, 2008). In mitochondria the ND5 gene has been shown to exhibit high variability (Simon et al., 1994; Zhou et al., 2003), and the speed of the evolved time is more rapid than for CO I and CO II (Yagi et al., 1999). Therefore, we proceeded to obtain a molecular phylogeny of Uropterygiinae eels in Taiwan derived from the analysis of the complete NADH dehydrogenase, subunit 5 gene sequences (1,842 bp) from the mitochondrial DNA. We amplified and analyzed the gene sequence for the phylogenetic relationship.

## MATERIALS AND METHODS

All moray eel specimens of subfamily Uropterygiinae were collected either by longline or by clove oil. Specimens used for morphological studies were preserved in 10% formalin for a week before being transferred into 70% ethanol for long-term preservation. The methods of measurement generally follow those of Böhlke (1982), Böhlke & Randall (2000) and Chen & Shao (1995). We borrowed specimens from the National Marine Science Museum (NMSMP), the Taiwan Fisheries Research Institute (FRIP), the Bernice P. Bishop Museum (BPBM), Honolulu, Hawaii and the National Museum of Natural History, United States (USNM). All Taiwanese type specimens were deposited in the Museum of the Biodiversity Research Center, Academia Sinica (ASIZP), and in the collection of the Laboratory of Aquatic Ecology, Department of Aquaculture, National Taiwan Ocean University (TOU-AE). The abbreviations of morphometric and meristic characters are as follows: TL, total length; HL, head length; DGO, depth at gill opening; S, snout length; TV, total vertebrae; MVF, mean vertebral formula.

The fresh specimens of subfamily Uropterygiinae to be used for molecular analysis were directly preserved in 95% ethanol when caught, frozen and transferred to the laboratory. A total of 15 specimens, comprising 4 genera and 7 Taiwanese muraenid species (without *Cirrimaxilla formosa*) were used in the molecular analysis and phylogenetic studies.

All DNA extractions of the Uropterygiinae specimens were carried out according to the general protocols of the High Pure PCR Template Preparation Kit (Roche) method. The 1,842 bp DNA fragments, including the full length of ND5 region, were amplified by polymerase chain reaction (PCR) using primers based on the flanking region that were designed from the conserved region sequences of the Anguilliformes in Genbank by second author (ISC). The primer and the

primer sequences of ND5 gene: five primers (SQMRleuD1, MRGlur1, ND5-MR, MRND5-D2 and ND5-leu) were used to amplify the complete mitochondrial ND5 genes by polymerase chain reaction (PCR) and sequencing. The 5 sets of primer sequences were SQMRleuD1: 5'-ACT CTT GTT GCA ACT CCA AG-3'; MRGlur1: 5'-ATA GTT GAA TTA CAA CGR TGG TTT TTC-3'; ND5-MR: 5'-CCT ATT TTK CGG ATG TCY TG-3'; MRND5-D2: 5'-CGR GCR GAC GCM AAC AC-3'; and ND5-leu: 5'-GAA CCA AAA ACT CTT GGT GCA ACT-3'.

PCR was carried out using an ABI Model 2720 thermal cycler (Applied Biosystems) set for 40–50 cycles. The 50 µL reaction volume contained 33.5µL of sterile distilled water, 5.0 µL of 10× PCR buffer (Takara), 4.0 µL of dNTP (2.5 mM each), 3.0 µL of MgCl<sub>2</sub> (2.5 mM), 1.0µL of each primer (10µM), 0.5µL of 2 unit Ex Taq Super-therm DNA polymerase and 2.0µL of template. The thermal cycle profile was as follows: denaturation at 94°C for 60 seconds, annealing at 49–51°C for 60 seconds and extension at 72°C for 90 seconds. A negative control without template DNA was carried out for each run of PCR. The PCR products were run on a 1.0% agarose gel (0.5× TBE buffer) gel electrophoresis and stained with ethidium bromide for band characterization under ultraviolet trans-illumination.

Double-stranded PCR products were purified using a High Pure PCR Product Purification Kit (Roche), before undergoing direct cycle sequencing with dye labeled terminators (ABI Big-Dye kit). All sequencing reactions were performed according to the manufacturer's instructions. Labeled fragments were analyzed using an ABI Model 3700 DNA sequencer. Nucleotide sequence alignment was done manually. The phylogenetic and molecular evolutionary analyses were conducted using Molecular Evolutionary Genetics Analysis (MEGA) version 4.0 (Kumar et al., 2004; Tamura et al., 2007) and PAUP 4.0\* (Phylogenetic Analysis Using Parsimony, vers. 4.0 b10) (Swofford, 2002) by neighbor-joining (NJ) and maximum parsimony (MP) methods with 1,000 bootstrap replications (Felsenstein, 1985). Bayesian analyses were conducted using MrBayes v3.1.2 (Huelsenbeck & Ronquist, 2001). Mrmodeltest selected GTR+I+G as the best-fit models of nucleotide substitutions for the 1<sup>st</sup>/2<sup>nd</sup>/3<sup>rd</sup> codon position. We assumed the model parameters in lset nst = 6 rates = invgamma. The Markov chain Monte Carlo (MCMC) process was set and continued the runs for 1.0×10<sup>7</sup> cycles, with 1 in every 1,000 trees being sampled.

## TAXONOMY

### Uropterygiinae Fowler, 1925

**Diagnosis.** – Dorsal and anal fins restricted to tail tip; teeth needle-like and pointed.

**Type genus.** – *Uropterygius* Rüppell, 1838

Table 1. Comparisons of range (average) of total length, proportions, vertebral counts among the five species of Uropterygiinae.

	<i>A. allardicei</i>	<i>Cha. vittata</i>	<i>Cir. formosa</i>	<i>S. marmorata</i>	<i>S. tigrina</i>
No. of specimens	4	1	1	3	13
Total length (mm)	116–154	722	166	430–631	557–1101
% of total length					
Tail length	50.6–51.5 (51.0)	33.4	38.4	57.0–57.4 (57.1)	33.6–37.0 (35.1)
Preanal length	48.5–49.4 (49.0)	66.6	61.6	42.6–43.0 (42.9)	63.0–66.4 (64.9)
Trunk length	35.1–39.4 (36.9)	50.3	45.4	33.6–34.1 (33.9)	55.9–59.5 (57.7)
Body depth at gill opening	4.4–5.8 (4.9)	7.3	6.1	3.0–4.0 (3.5)	2.5–3.5 (3.0)
% of head length					
Snout length	13.2–15.8 (14.9)	7.8	13.3	14.0–15.2 (14.6)	12.5–17.1 (15.1)
Eye diameter	7.1–11.3 (8.7)	3.0	6.5	5.6–6.7 (6.1)	5.3–7.3 (6.4)
In total length					
Tail length	1.9–2.0 (2.0)	3.0	2.6	1.7–1.8 (1.7)	2.7–3.0 (2.9)
Trunk length	2.7–2.9 (2.8)	2.0	2.2	2.9–3.0 (3.0)	1.7–1.8 (1.7)
Body depth at anus	19.6–23.8 (22.0)	10.0	13.2	29.2–35.8 (32.5)	44.5–50.5 (47.0)
Body depth at gill opening	18.0–22.8 (21.2)	13.7	16.4	24.8–33.7 (29.2)	30.8–38.8 (34.7)
Head length	7.0–8.0 (7.6)	6.3	6.3	10.9–11.1 (11.0)	12.4–13.9 (13.4)
In head length					
Upper Jaw length	3.0–3.1 (3.1)	2.1	2.6	2.5–2.7 (2.6)	2.6–3.8 (2.9)
Lower Jaw length	3.0–3.1 (3.1)	2.1	2.8	2.7–2.7 (2.7)	2.6–3.3 (2.9)
Snout length	6.3–7.6 (6.8)	12.8	7.5	6.6–7.2 (6.9)	6.2–7.5 (6.6)
Eye diameter	8.0–13.2 (10.0)	33.3	15.5	15.1–18.0 (16.5)	13.7–18.5 (15.8)
Interorbital width	6.5–10.9 (8.1)	12.8	9.1	7.6–10.1 (8.9)	5.6–7.9 (6.6)
Counts					
Total vertebrae	91–101 (96)	154	132	132–134	164–171 (167)
Predorsal vertebrae	81–91 (86)	122	114	121–122	158–162 (160)
Preanal vertebrae	83–92 (88)	123	117	122–123	160–164 (162)
Pre-epipleural vertebrae	56	76	76	27–30	11–15 (13)
PAV-PDV	1–3	1	3	1	1–4 (2)
TV-PAV	8–10	31	15	11	4–9 (7)

*A*, *Anarchias*; *Cha*, *Channomuraena*; *Cir*, *Cirrimaxilla*; *S*, *Scuticaria*.

### *Anarchias* Jordon & Starks, 1906

*Type species.* – *Anarchias allardicei* Jordan & Starks, 1906.

#### *Anarchias allardicei* Jordan & Starks, 1906

##### Allardice's moray

(Fig. 1A)

*Anarchias allardicei* Jordan & Starks in Jordan & Seale, 1906: 204. (Pago Pago, Samoa); Schultz et al., 1953: 143; Chen et al., 1994: 54.

*Material examined.* – Four specimens (116–154 mm TL). NMSMP 885, 125 mm TL, Tungchi, Aug.1991; NMSMP 1013, 116 mm TL, Wanlitung, Aug.1992; TOU-AE 1780, 124 mm TL, clove oil, tidal pool of Hsiaogang, Chenkung, Taitung, Oct.2005. TOU-AE 4913, 154 mm TL, clove oil, tidal pool of Jihuei, Chenkung, Taitung, May 2008.

*Diagnosis.* – A small species of *Anarchias*, distinguished by posterior nostril appearing as a double pore. Head length 7.0–8.0 (7.6), depth at gill opening 18.0–22.8 (21.2), trunk length 2.7–2.9 (2.8), all in total length; eye diameter 8.0–13.2 (10.0), snout length 6.3–7.6 (6.8), all in head

length; total vertebrae 91–101 (96) (Table 1). Two branched pores. Mostly uniformly pale brown when fresh, dorsal area darker. Yellowish tail tip when alive, turning white after death. Whitish oral cavity, cephalic pores, posterior nostril and anus.

*Distribution.* – Indo-Pacific: Chagos Islands to the Society Islands, south to the southern Great Barrier Reef. Taiwan: Tungchi, Penghu, Wanlitung, Kenting, Lanyu, Hsiaogang and Chengkung.

### *Channomuraena* Richardson, 1848

*Type species.* – *Ichthyophis vittata* Richardson, 1845.

#### *Channomuraena vittata* (Richardson, 1845)

##### Broadbanded moray

(Fig. 1B)

*Ichthyophis vittatus* Richardson, 1845: 114, Pl. 53 (brought from China).

*Nettastoma vittata* – Richardson, 1848: 96.

*Channomuraena vittata* – Richardson, 1848: 96.

*Channomuraena vittata* – Kaup, 1856: 66; Böhlke et al., 1989: 122.

*Gymnomuraena vittata* – Günther, 1870: 134.

**Material examined.** – TOU-AE 4911, 722 mm TL, Chengkung, Jan.1997.

**Diagnosis.** – A rare moray eel. Lower jaw notably longer than upper jaw, eye above anterior third of jaws. Tail length about 3 in total length. Body pale with 13–16 irregular dark bars. Head length 6.3, depth at gill opening 13.7, trunk length 2.0, all in total length; eye diameter 33.3, snout length 12.8, all in head length; total vertebrae 154.

**Distribution.** – Indian Ocean: Réunion and Mauritius and Christmas Island. Western Pacific: Palau, and the Hawaiian Islands. Western Atlantic: Bermuda, Bahamas, and Caribbean Sea. Taiwan: Chengkung.

**Remarks.** – Although Richardson (1845) notes that the holotype specimen of *Channomuraena vittata* was brought from China it is an unusual moray eel in that it has been recorded from both the Pacific and the Atlantic. But during the 153 years until the present, it has not been recorded again from China, Japan, Indonesia or the nearby seas. In 1997, the first Taiwanese specimen TOU-AE 4911 of this species was collected in Chengkung. The second Taiwanese specimen (FRIP 21996, 1,270 mm TL) was collected from Hsiaogang, Taitung on 22 Sep.2006. We therefore verify that China can indeed be the type locality.

#### ***Cirrimaxilla* Chen & Shao, 1995**

**Type species.** – *Cirrimaxilla formosa* Chen & Shao, 1995.

#### ***Cirrimaxilla formosa* Chen & Shao, 1995 Taiwanese barbel moray (Fig. 1C)**

*Cirrimaxilla formosa* Chen & Shao, 1995: 328; Böhlke & Smith, 2002: 158.

**Material examined.** – Holotype: ASIZP 056729, 166 mm TL, Nanwan, Jun.1987.

**Diagnosis.** – A small species of *Cirrimaxilla*. Margin of both jaws with many cirri, rim of posterior nostril petal-like. Obscure branchial pore, hooked fang-like teeth, body tawny with numerous brown tiger-like bands, tail shorter than trunk. Head length 6.3, depth at gill opening 16.4, trunk length 2.2, all in total length; eye diameter 15.5, snout length 7.5, all in head length; total vertebrae 132.

**Distribution.** – Known from the type locality, Nan-wan, Kenting National Park, Ping-tung, the southern-most County of Taiwan; New Caledonia.

**Remarks.** – Séret et al. (2008) recorded 16 specimens of *C. formosa* were found in the stomachs of the sea snakes

*Laticauda latauda* and *L. saintgieonsi* collected in New Caledonia during an ecological study on the sea snakes. However, *C. formosa* in Taiwan was very rare, it might be due to the predation of sea snakes.

#### ***Scuticaria* Jordan & Snyder, 1901**

**Type species.** – *Ichthyophis tigrinus* Lesson, 1828: 399. (not seen)

#### ***Scuticaria tigrina* (Lesson, 1828)**

##### **Tiger reef-eel**

(Fig. 1D)

*Ichthyophis tigrinus* Lesson, 1828: 399 (Borabora, Society Island)

*Muraenoblenna tigrina* – Kaup, 1856: 66.

*Gymnomuraena tigrina* – Bleeker, 1864: 113; Günther, 1870: 133.

*Scuticaria tigrina* – Jordan & Snyder, 1901: 886; Jordan & Seale, 1906: 206; Böhlke et al., 1989: 117; Böhlke & McCosker, 1997: 171; Böhlke & Randall, 2000: 265–266, Pl. VI.-A

*Uropterygius tigrinus* – Smith, 1962: 426; Tinker, 1991: 117; Castle & McCosker, 1986: 175; Chen et al., 1994: 63; Yamakawa et al., 1994: 2–5, Figs 1–3.

*Uropterygius (Scuticaria) tigrinus* – Myers, 1989: 50, Pl. 10H.

**Material examined.** – Thirteen specimens (557–1,101 mm TL). ASIZP 056524, 870 mm TL, Wanlitung, May 1986; TOU-AE0296, 936 mm TL, Sanshengtai, Jul.2003; TOU-AE0382, 790 mm TL, Chengkung, Oct.2003; TOU-AE1334, 557 mm TL, Shueilian, Jul.2005; 2 (868–1,101 mm TL): Sanshengtai, May 2006, TOU-AE1871, 1,101 mm TL; TOU-AE2022, 868 mm TL; 4 (641–936 mm TL): Shihtigang, May 2006, TOU-AE1977, 936 mm TL; Jun.2006, TOU-AE2228, 861 mm TL; Jul.2006, TOU-AE2336, 641 mm TL; Jul.2006, TOU-AE2337; 3 (635–794 mm TL): Sep.2006, TOU-AE3245, 794 mm TL; Jul.2007, TOU-AE3681, 635 mm TL; Aug.2007, TOU-AE4276, 791 mm TL.

**Diagnosis.** – An elongate, large, near-cylindrical moray. Inter-muscular bones thick. Jaw teeth bi-serial. Posterior nostrils tubular, equal to anterior nostril in length, all are whitish. One branchial pore. Tail length about 3 in total length. Generally yellow to orange body, blotched with roundish dark-brown spots. Head length 12.4–13.9 (13.4), depth at gill opening 30.8–38.8 (34.7), trunk length 1.7–1.8 (1.7), all in total length; eye diameter 13.7–18.5 (15.8), snout length 6.2–7.5 (6.6), all in head length. MVF 160–162–167, total vertebrae 164–171 (167).

**Distribution.** – Indo-Pacific: East Africa to the Society Islands, north to the Philippines, Japan and the Hawaiian Islands. Eastern central Pacific: Mexico, Costa Rica, and Panama. Taiwan: Wanlitung, Taitung.

**Remarks.** – This species is easily characterized by the position of the longer posterior nostrils. The counts of the numerous vertebrae, MVF 160–162–167 (164–171), exceed those of the type species *Uropterygius concolor* Rüppell, 1838 with MVF 109–111–119 (118–123). Chen et al. (1994) adopted the synonym *Uropterygius tigrinus* because many



Fig. 1. The species of Uropterygiinae in Taiwan. A, *Anarchias allardicei*, NMSMP 1013, 116 mm TL; B, *Channomuraena vitata*, TOU-AE 4911, 722 mm TL; C, *Cirrimaxilla formosa*, ASIZP 056729, 166 mm TL; D, *Scuticaria tigrina*, TOU-AE0382, 790 mm; E, *Scuticaria marmorata*, TOU-AE 4827, 631 mm TL; F, *Uropterygius macrocephalus*, TOU-AE 0331, 265 mm TL; G, *Uropterygius micropterus*, TOU-AE 0346, 247 mm TL; H, *Uropterygius oligospondylus* new species, Holotype, male, TOU-AE 1862, 448 mm TL.

of its features as snout, dentition and fins are similar to those of *Uropterygius*. However, Chen et al. (1997) changed its genus to *Scuticaria* because it could grow to 105 cm TL with a feature of shorter tail unlike most species of *Uropterygius*.

***Scuticaria marmorata* (Lacepède, 1803)  
Marbled reef-eel  
(Fig. 1E)**

*Gymnomuraena marmorata* Lacepède, 1803: 648–650. (No type found)

*Uropterygius marmoratus* – Böhlke & Smith, 2002: 161–162; Böhlke & Randall, 2000: 270, Pl. VI.-D.

**Material examined.** – Three specimens (430–631 mm TL). TOU-AE 1767, 430 mm TL, Taitung, Oct.2005; TOU-AE 3197, 586 mm TL, Lanyu, Aug.2006. TOU-AE 4827, 631 mm TL, Lanyu, Jul.2006.

**Diagnosis.** – An elongate, near cylindrical moray. Intermuscular bones thick. Ground colour cream to grey, densely mottled with numerous closely-set dark rounded spots. Anterior nostril in short to moderate tube, posterior nostril above mid-eye, gill opening a small slit about at mid-side. One small branchial pore. Dorsal and anal fins confined to tail tip. Jaw teeth tri-serial, vomerine teeth partially bi-serial. Head length 10.9–11.1 (11.0), depth at gill opening 24.8–33.7 (29.2), trunk length 2.9–3.0 (3.0), all in total length; eye diameter 15.1–18.0 (16.5), snout length 6.6–7.2 (6.9), all in head length; total vertebrae 132–134.

**Distribution.** – Indo-Pacific: East Africa to the Hawaiian, Marquesan and Tuamotu Archipelago, north to the Yaeyamas, south to Tonga. Taiwan: Lanyu, Chengkung.

**Remarks.** – This species grow to moderately large size with our largest specimen measuring 631 mm TL. In the genus *Uropterygius*, adults may be small to medium in size, and the type species *Uropterygius concolor* Rüppell, 1838, had MVF 109–111–119, Total vertebrae 118–123. The species of so-called “*Uropterygius*” *marmoratus* MVF 122–123–134, Total vertebrae 132–134 and most species of *Uropterygius* did not exceed 400 mm TL. The intermuscular bones (epineural ribs (EN) and epipleural ribs (EP)) of *S. marmorata* are similar to *S. tigrina* which also had thick intermuscular bones (Fig. 2). The characteristics of ND5 sequence analysis in NJ and Bayesian tree provided evidence that the genetic distance of *S. marmorata* differed from those of the other three species of *Uropterygius*. After we re-examined the specimens, we concluded that this species should be moved to its sister genus, *Scuticaria* (Lesson, 1828).

***Uropterygius* Rüppell, 1838**

**Type species.** – *Uropterygius concolor* Rüppell, 1838.

***Uropterygius macrocephalus* (Bleeker, 1864)  
Needle-tooth moray  
(Fig. 1F)**

*Gymnomuraena macrocephalus* Bleeker, 1864: 114 (Amboina, Indonesia).

*Uropterygius reidi* – Schultz, 1943: 32, pl. 5 (Samoa).

*Uropterygius macrocephalus* – Hatooka, 1984: 26; McCosker et al., 1984: 263; Böhlke & Randall, 2000: 269, Pl. VI.-C.

**Material examined.** – Nine specimens (273–377 mm TL). NMSMP 25, 364 mm TL, Lanyu, Aug.1978; 6 (273–377 mm TL), Changbin, Sep.2006, TOU-AE 3210, 335 mm; TOU-AE 3211, 353 mm; TOU-AE 3212, 377 mm; TOU-AE 3220, 289 mm; TOU-AE 3221, 283 mm; TOU-AE 3222, 273 mm; TOU-AE 2883, 332 mm TL, Changbin, Jun.2006; TOU-AE 2748, 325 mm TL, Changbin, Jul.2006.

**Diagnosis.** – A small species of *Uropterygius*. Black or black-brown body, sometimes black-green when alive, with many brown snowflake blotches all over the body. Whitish cephalic pores. Posterior nostrils short, tubular-like. Swollen nasal cavity. Teeth biserial. Head length 6.9–7.9 (7.3), depth at gill opening 21.1–27.0 (23.3), trunk length 2.8–3.1 (2.9), all in total length; eye diameter 17.3–19.3 (18.4), snout length 5.3–6.6 (5.8), all in head length; total vertebrae 109–115 (112).

**Distribution.** – Indo-Pacific: Réunion and Mauritius, Seychelles, Christmas Island to the Society Islands, north to southern Japan and the Hawaiian Islands. Eastern Pacific: southern Gulf of California to Ecuador, including the Revillagigedo, Cocos and Galapagos Islands. Taiwan: Taitung, Kenting and Keelung.

***Uropterygius micropterus* (Bleeker, 1852)  
Tidepool snake moray  
(Fig. 1G)**

*Muraena micropterus* Bleeker, 1852: 298 (Ceram, Indonesia)

*Uropterygius micropterus* – Hatooka, 1984: 26; McCosker et al., 1984: 265.

**Material examined.** – Nine specimens (113–265 mm TL). NMSMP 918, 180 mm TL, Maopitou, Aug.1991; TOU-AE 0502, 227 mm, Hsiogang, Oct.2003; TOU-AE 1844, 262 mm, Chengkung, Mar.2006; TOU-AE 1975, 194 mm, Jihuei, Jun.2006; 4 (113–265 mm TL): Jihuei, Aug.2006, TOU-AE 2840, 113 mm; TOU-AE 2959, 265 mm; TOU-AE 2960, 251 mm; TOU-AE 2961, 187 mm; TOU-AE 3820, 258 mm, Lanyu, Jul.2007.

**Diagnosis.** – A small species of *Uropterygius*. Pale lower head and body parts, grey-brown with a network of web-like brownish thin lines. Teeth biserial. Head length 8.9–10.2 (9.4), depth at gill opening 30.5–35.6 (33.5), trunk length 2.6–2.9 (2.8), all in total length; eye diameter 12.7–16.8 (14.0), snout length 7.4–9.3 (8.3), all in head length; total vertebrae 115–118 (116).

**Distribution.** – Indo-Pacific: East Africa to Samoa, north to southern Japan, south to the southern Great Barrier Reef,

Marianas in Micronesia. Taiwan: Hsiaoliuchiou, Kenting, Taitung, Lutao and Lanyu.

**Remarks.** – Many specimens of this species in Taiwan were misidentified as “*U. marmoratus*”. In fact, skin coloration differs between these two species. *Scuticaria marmorata* has round dots on the body instead of the netted coloration in *U. micropterus*.

***Uropterygius oligospondylus*, H. M. Chen,  
J. E. Randall & K. H. Loh, new species  
Few-vertebrae moray  
(Figs. 1H, 3 & 4; Table 2)**

**Material examined.** – Holotype: TOU-AE 1862, 448 mm TL, male, off shore of Changbin, Taitung, Taiwan, 23.311°N 121.453°E, 15 m, longline, Captain Jiunn-Shiun Chiou, 01 Jun.2006. Paratypes: BPBM 16129 (originally identified as *Uropterygius cf macrocephalus*), 429 mm TL, Savo, Solomon Islands, rocky shore, 0–1 meter, rotenone, coll. Randall, J.E., B. Goldman & L. Goldman, Jul.1973. USNM 352431, 535 mm TL. Pacific, Vanuatu, Tanna Island, Port Resolution, 0–3 meter, rotenone, Jun.1996.

**Diagnosis.** – Body depth higher, fewer vertebrae 100–103, grey body color, blackish reticular pattern, jaws teeth in three rows, denser dentition, teeth longer. Anus close to mid-body point. Head length 6.4–7.3, depth at gill opening 12.0–15.5, Trunk length 2.7–2.8, all in total length; eye diameter 21.4–23.3, snout length 4.9–6.2, all in head length.

**Description.** – Table 2 presents the proportions as percentage of total length or head length, vertebral counts and gonadal type of the holotype and paratypes. The values are listed in the following range: tail length 2.0, trunk length 2.7–2.8, depth at anus 14.1–16.0, depth at gill opening 12.0–15.5, head length 6.4–7.3, all in total length. Proportions in percent of head: upper jaw length 2.3–2.8, lower jaw length 2.4–2.8, snout length 4.9–6.2, eye diameter 21.4–23.3, inter-orbital width 6.6–7.8. Pre-dorsal vertebrae 79–81, pre-anal vertebrae 83–85 and total vertebrae 100–103. The radiograph of the holotype specimen (Fig. 3) shows the entire skeleton.

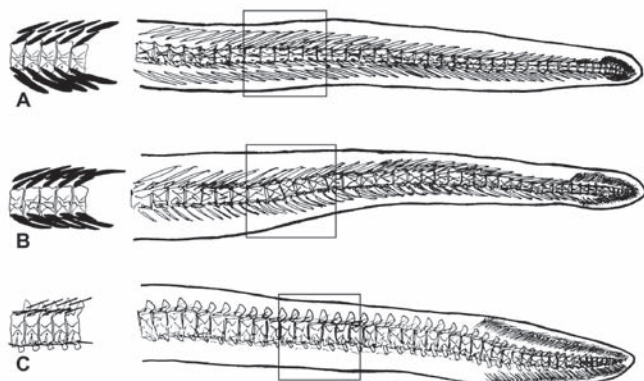


Fig. 2. Morphological comparison of inter-muscular bones (on the 30–35<sup>th</sup> vertebrae count from the end), vertebrae and caudal fin rays (including relative pterygiophores) from three Uropterygiinae species: A, *Scuticaria tigrina*, TOU-AE 2022, 868 mm TL; B, *Scuticaria marmorata*, TOU-AE 4827, 631 mm TL; C, *Uropterygius oligospondylus*, TOU-AE 1862, 448 mm TL.

Mouth in terminal position and closing completely. Holotype and paratype dentition is shown in Fig. 5, with the values listed in the following range: Intermaxillary teeth plate with 13–20 teeth forming 3–4 irregular rows. Premaxillary teeth plate with 14–17 teeth. Maxillary teeth tri-serial; outer row in the left 39–52, in the right 35–56 small teeth and inner row in the left 16–18, in the right 12–18 slender fangs. Vomerine teeth plate with 9 teeth forming irregular uni-serial row. Dentary teeth biserial to triserial, outer row small, closely-set, with about 36–69 in the left and 28–67 in the right, inner row teeth larger about 23–24 in the left and 22–23 in the right.

Body very stout, dorsal and anal fins restricted to end of tail. Anterior nostrils are tubular on each side of snout tip. Posterior nostrils are short tubular in the mid-point of eye. Head pores typical of the genus: supra-orbital canal with three pores, infra-orbital canal with four pores, the first just behind anterior nostril, the last below posterior margin of eye; six pores in mandibular. One small branchial pore (difficult to discern) above and well before gill opening. Gill opening just below longitudinal midline of body.

**Colour.** – Grey to brownish body colour, blackish reticular pattern. In alcohol or formalin also grey brownish body colour with blackish reticular or vertical bars. Lower jaw brownish. Corners of mouth and inner mouth side similar to body colour.

**Distribution.** – From southeastern Taiwan, Solomon Islands and Vanuatu.

**Etymology.** – The species name is from the Greek *oligo* (few) and *spondylos* (vertebrae), in reference to its lower vertebral count.

**Remarks.** – According to the data for the type specimens of Indo-Pacific Muraenidae (Böhlke & Smith, 2002) and also the web site of FishBase (Froese & Pauly, 2008), 41 species belong to the genus *Uropterygius* in the world, but only 20 of them are currently considered valid (Böhlke & Smith, 2002). This new species, *Uropterygius oligospondylus*, is distinct from all the other congeners, with the lowest count of vertebral formula (MVF 80-84-101), as total vertebrae 100–103. *Uropterygius oligospondylus* seems to be most close to *U. macrocephalus* in terms of similar body shape and pigmentation pattern. However, *Uropterygius oligospondylus*, new species, is clearly distinguishable from *U. macrocephalus* (Bleeker, 1864) by the following features: (1) greater body depth DGO 7.3 (vs. 4.6% of TL); (2) fewer vertebrae MVF 80-84-101 (vs. 90-94-112) (Table 1); (3) body background grey (vs. black or blackish brown); (4) blackish reticular pattern (vs. brown snowflake pattern); and (5) jaws teeth in tri-serial (vs. bi-serial).

Table 2. Comparisons of range (average) of total length, proportions, vertebral counts of the holotype and two paratypes of *Uropterygius oligospondylus* new species with other two species of *Uropterygius* in Taiwan.

Type status No. of specimens	<i>U. oligospondylus</i>			<i>U. macrocephalus</i>	<i>U. micropterus</i>
	H 1	P 2	H + P 3	N 9	N 9
Total length (mm)	448	429–535	429–535	273–377	113–265
% of total length					
Tail length	51.1	49.2–51.0	49.2–51.1 (50.4)	51.5–53.6 (52.5)	51.6–57.2 (53.9)
Preanal length	48.9	49.0–50.8	48.9–50.8 (49.6)	46.4–48.5 (47.5)	42.8–48.4 (46.1)
Trunk length	36.6	35.3–35.9	35.3–36.6 (35.9)	33.7–36.4 (34.5)	35.1–39.2 (36.5)
Body depth at gill opening	6.5	7.1–8.3	6.5–8.3 (7.3)	3.7–5.4 (4.6)	2.1–4.7 (3.3)
% of head length					
Snout length	20.3	16.2–18.2	16.2–20.3 (18.2)	15.8–18.8 (17.6)	10.0–14.9 (12.2)
Eye diameter	4.3	4.3–4.7	4.3–4.7 (4.4)	5.2–6.0 (5.5)	4.2–7.9 (6.5)
In total length					
Tail length	2.0	2.0	2.0	1.9	1.8–1.9 (1.9)
Trunk length	2.7	2.8	2.7–2.8 (2.8)	2.8–3.1 (2.9)	2.6–2.9 (2.8)
Body depth at anus	16.0	14.1–14.4	14.1–16.0 (14.8)	25.2–30.3 (27.4)	31.8–34.4 (32.8)
Body depth at gill opening	15.5	12.0–14.2	12.0–15.5 (13.9)	21.1–27.0 (23.3)	30.5–35.6 (33.5)
Head length	7.1	6.4–7.3	6.4–7.3 (6.9)	6.9–7.9 (7.3)	8.9–10.2 (9.4)
In head length					
Upper Jaw length	2.3	2.7–2.8	2.3–2.8 (2.6)	2.2–2.9 (2.4)	2.6–3.3 (2.9)
Lower Jaw length	2.4	2.7–2.8	2.4–2.8 (2.7)	2.3–2.9 (2.6)	2.8–3.6 (3.0)
Snout length	4.9	5.5–6.2	4.9–6.2 (5.5)	5.3–6.6 (5.8)	7.4–9.3 (8.3)
Eye diameter	23.3	21.4–23.1	21.4–23.3 (22.6)	17.3–19.3 (18.4)	12.7–16.8 (14.0)
Interorbital width	6.6	6.8–7.8	6.6–7.8 (7.0)	7.1–9.5 (8.3)	5.7–9.2 (7.0)
Counts					
Total vertebrae	101	100–103	100–103 (101)	109–115 (112)	115–118 (116)
Predorsal vertebrae	81	79–81	79–81 (80)	88–92 (90)	103–106 (104)
Preanal vertebrae	85	83–85	83–85 (84)	93–96 (94)	105–108 (106)
Pre-epipleural vertebrae	50	55	50–55	45–48 (46)	48–56 (52)
PAV-PDV	4	4	4 (4)	4–5 (5)	2–3 (2)
TV-PAV	16	17–18	16–18 (17)	15–19 (17)	8–10 (10)

H, Holotype; P, Paratype; N, Nontype.

**Key to the species of subfamily Uropterygiinae occurring in Taiwanese waters**

1. Posterior nostril adjacent with an enlarged supra-orbital pore, the 2 appearing as a double pore; MVF 86-88-96 ..... *Anarchias allardicei*
- Posterior nostril a single pore ..... 2
2. Snout very short (HL/S > 11); lower jaw notably longer than upper jaw, body pale with irregular dark bars, MVF 122-123-154 ..... *Channomuraena vittata*
- Snout moderate (HL/S < 11) ..... 3
3. Margin of both jaws with many cirri, tail shorter than trunk, lower jaw protruding, MVF 114-117-132 ..... *Cirrimaxilla formosa*
- Margin of both jaws without any cirri ..... 4
4. Tail more stiff, intermuscular bones thick, body more elongate and nearly cylindrical ..... *Scuticaria* 5
- Tail less stiff, intermuscular bones thin, body less elongate... ..... *Uropterygius* 6
5. Ground colour cream to grey, densely mottled with numerous close-set dark, rounded spots; MVF 122-123-134 ..... *S. marmorata*
- Ground colour light tan to yellowish, overlaid with prominent dark spots or blotches; MVF 160-162-167 ..... *S. tigrina*
6. TL/DGO < 16, TV < 105; Colour grey, posterior nostrils over middle or posterior part of eye, to 45 cm, MVF 80-84-101 ..... *U. oligospondylus*
- TL/DGO > 17, TV > 105; anus near mid-length, tail length about 2 or less in TL ..... 7
7. Colour pale to grey, posterior nostril over front of eye; mottled with thin dark brown reticulated network; to 30 cm; MVF 104-106- 116 ..... *U. micropterus*

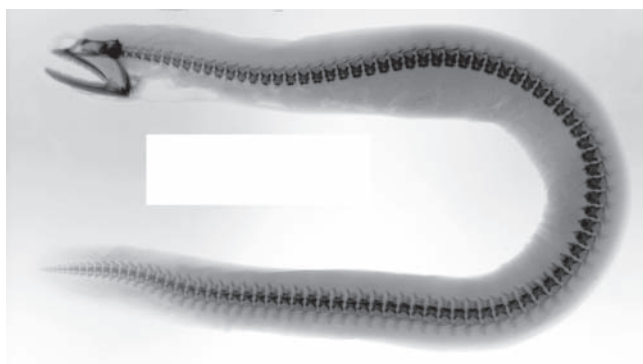


Fig. 3. Radiograph from the holotype (TOU-AE1862) of *Uropterygius oligospondylus* new species.



- Colour blackish, posterior nostril above or behind middle of eye; with thick brown network; to 40 cm; MVF 91-93-115 ..... *U. macrocephalus*

**MOLECULAR PHYLOGENETIC ANALYSIS**

The ND5 mitochondrial gene with 1,842 bp was amplified successfully for all the seven species of subfamily Uropterygiinae samples from a total of 15 individuals (Table 3), and there is no insertion or deletion. The ND5 gene is with 614 amino acid codings, and the aligned sequences with 706 divergent sites were variable in all seven species of Uropterygiinae (Appendix I). The average frequencies of nucleotides for all taxa of Uropterygiinae are as follows: A = 29.5%; C = 30.3%; G = 15.0%; T = 25.2%. Nucleotide sequences in ND5 gene of Uropterygiinae are slightly AT-rich (53.2–56.2%) (Table 4). The numbers of transitions (Ti) were higher than those of transversions (Tv), and the average ratio of Ti / Tv was 1.8.

All trees of NJ, MP and Bayesian analyses based on GTR+ I + G model distance in molecular phylogenetic analyses are with *Gymnothorax kidako*, *Anguilla japonica* and *Conger myriaster* as outgroups. The result of pair-wise genetic affinity suggests that *U. oligospondylus* was distinct from the other two *Uropterygius* species, and it can be supported genetically as a new species.

Neighbor-joining analysis (Fig. 6) supported the different genera of subfamily Uropterygiinae by high confidence levels in 65–100% of bootstrap replications. The species of *Scuticaria tigrina* and so-called “*Uropterygius*” *marmoratus* (Lacepède) were sister species for 69% of bootstrap replications.

Maximum-parsimony (MP) analysis, using equal weighting and including all positions with heuristic search, resulted in two MP tree with tree length = 2,433, CI = 0.588, and RI = 0.671 (Fig. 7). Apparently so-called “*Uropterygius*” *marmoratus* (Lacepède) does not belong the genus *Uropterygius*.

Bayesian analyses based on GTR+ I +G model (Fig. 8) indicated that *Scuticaria tigrina* and so-called “*Uropterygius*” *marmoratus* (Lacepède) are sister species (supported with high Bayesian posterior probability of 100%). The result also supports that the genera *Uropterygius* and *Scuticaria* are sister-groups.

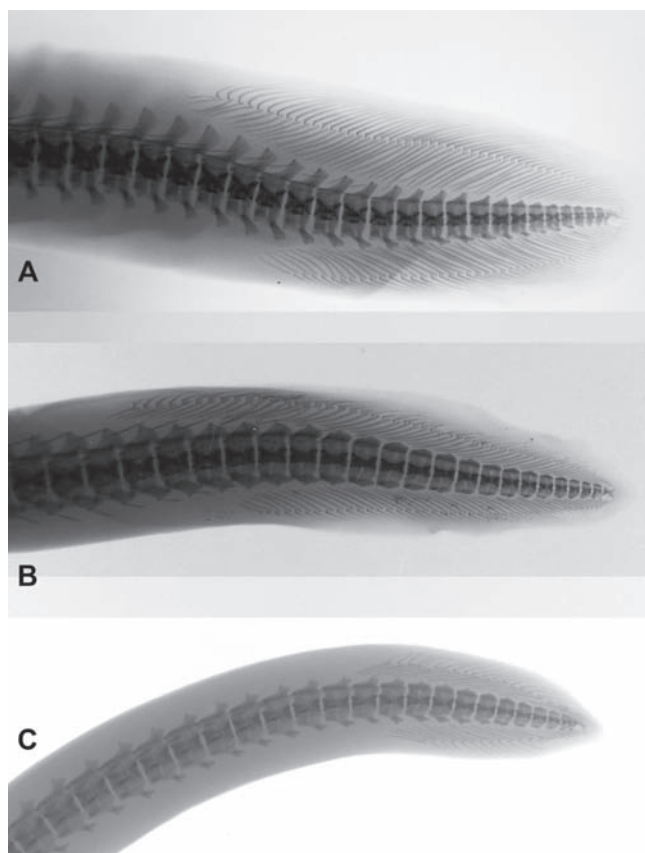


Fig. 4. Radiographs from the tail tips: A, *Uropterygius oligospondylus*, TOU-AE 1862, 448 mm TL; B, *U. macrocephalus*, TOU-AE 3218, 317 mm TL; C, *U. micropterus*, TOU-AE 4918, 295 mm TL.

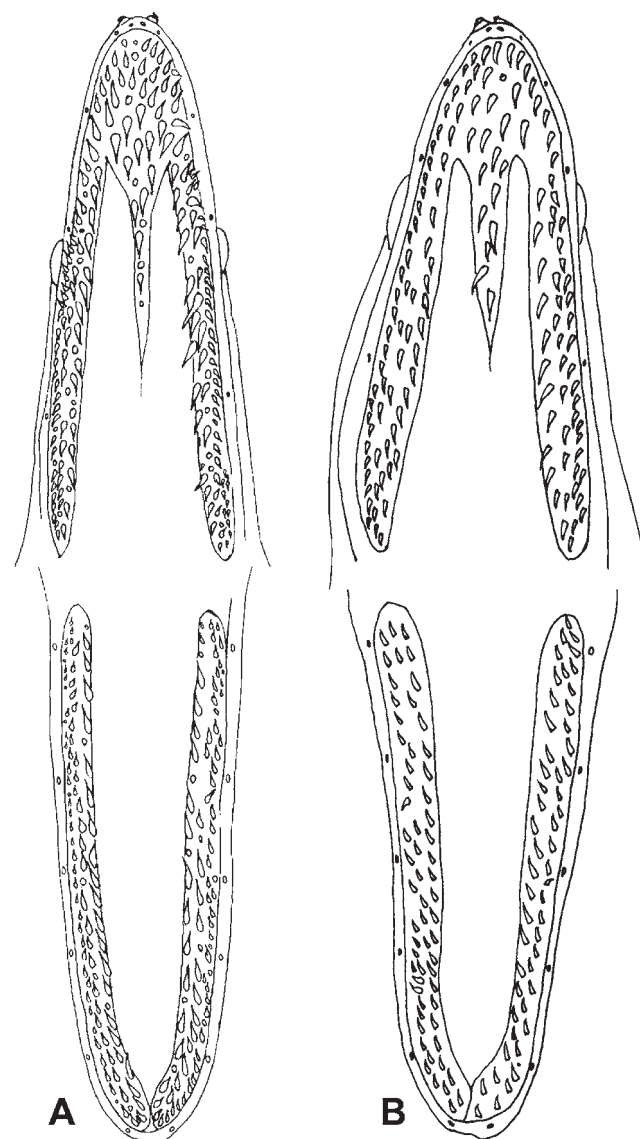


Fig. 5. Dentitions from the type specimens of *Uropterygius oligospondylus* new species: A, holotype, male, TOU-AE 1862, 448 mm TL; B, paratype, BPBM 16129, 429 mm TL.

Table 3. The collecting localities and catalogue numbers of muraenid specimens for mtDNA analysis.

OTUs	Scientific name	Locality	Specimen number
Aall	<i>Anarchias allardicei</i>	Lutao	TOU-AE 4912
Chvit	<i>Channomuraena vittata</i>	Hsiaogang	FRIP 21996
Umac1	<i>Uropterygius macrocephalus</i>	Jihuei	TOU-AE 3215
Umac2	<i>Uropterygius macrocephalus</i>	Jihuei	TOU-AE 3216
Umac3	<i>Uropterygius macrocephalus</i>	Changbin	TOU-AE 3212
Umic1	<i>Uropterygius micropterus</i>	Jihuei	TOU-AE 2840
Umic2	<i>Uropterygius micropterus</i>	Chengkung	TOU-AE 1975
Umic3	<i>Uropterygius micropterus</i>	Hsiaogang	TOU-AE 1844
Uoli	<i>Uropterygius oligospondylus</i>	Changbin	TOU-AE 1862
Smar1	<i>Scuticaria marmorata</i>	Lanyu	TOU-AE 3197
Smar2	<i>Scuticaria marmorata</i>	Taitung	TOU-AE 1767
Smar3	<i>Scuticaria marmorata</i>	Lanyu	TOU-AE 4917
Stig1	<i>Scuticaria tigrina</i>	Shihtigang	TOU-AE 3245
Stig2	<i>Scuticaria tigrina</i>	Shihtigang	TOU-AE 2337
Stig3	<i>Scuticaria tigrina</i>	Shihtigang	TOU-AE 2336

Table 4. Percentages of base composition of nucleotide substitution of mtDNA ND5 sequence data of 10 species. The species marked with an \* are the average value (n = 3).

Scientific name	Nucleotide (%)					
	A	T	C	G	A+T	C+G
<i>Uropterygius macrocephalus</i> *	29.0	25.5	30.4	15.1	54.5	45.5
<i>Uropterygius micropterus</i> *	29.4	25.9	30.3	14.5	55.3	44.8
<i>Uropterygius oligospondylus</i>	30.7	25.5	29.8	14.1	56.2	43.9
<i>Scuticaria marmorata</i> *	30.3	25.8	29.5	14.3	56.1	43.8
<i>Scuticaria tigrina</i> *	29.2	24.2	30.8	14.7	53.4	46.5
<i>Anarchias allardicei</i>	31.0	24.6	29.3	15.1	55.6	44.4
<i>Channomuraena vittata</i>	28.3	24.9	31.3	15.5	53.2	46.8
<i>Gymnothorax kidako</i>	30.5	28.1	26.9	14.5	58.6	41.4
<i>Anguilla japonica</i>	35.1	26.4	25.7	12.8	61.5	38.5
<i>Conger myriaster</i>	35.0	28.2	24.2	12.6	63.2	36.8

Based on the common conclusion of NJ, MP and Bayesian analyses (Figs 6, 7 & 8), three phylogenetic trees share congruent support for the monophyly of the Uropterygiinae species in relation to *Gymnothorax kidako* by high confidence levels 94–100% of bootstrap replications (NJ and MP), and 100% posterior probability (Bayesian analysis). *Uropterygius macrocephalus*, *U. micropterus* and *U. oligospondylus* fall within the same clade (by high confidence levels 99–100% of bootstrap replications (NJ and MP), and 67% posterior probability (Bayesian analysis)).

## DISCUSSION

Sequence length of the ND5 mitochondrial gene was very consistently 1,842 bp and for the subfamily Uropterygiinae in the current study there is no insertion or deletion in the sequence alignment. The employment of this gene has the advantage of easy amplification by conserved primer set designed by us for all available members of this eel family (Loh et al., unpublished). The ND5 gene sequences from the following taxa of outgroups: *Anguilla japonica* (Japanese eel) (NC002707), *Conger myriaster* (conger eel) (AB038381), *Gymnothorax kidako* (moray eel) (AB049980) from the

GenBank also shared the same length of 1,842 bp. Nucleotide sequences in ND5 of different genera in Uropterygiinae (Muraenidae) are AT-content 53.2–56.2% and that of *Gymnothorax kidako* in Muraeninae (Muraenidae) is 58.6%, which are lower than other member in different families of eels including *A. japonica* (61.5%) (Anguillidae) and *C. myriaster* (63.2%) (Congridae). However, this preliminary findings still need further more Muraeninae species to test the current conclusion.

Based on the outgroup assignment of *Anguilla japonica* and *Conger myriaster*, the phylogenetic analysis seems to be gather the congruent result of overall topology. According to the NJ, MP and Bayesian analyses (Figs 6, 7 & 8), the phylogenetic trees share the congruent support for interspecific classification of subfamily Uropterygiinae, and show monophyly of the Uropterygiinae species in relation to *Gymnothorax kidako*. The same relationships may be discerned in both Muraeninae and Uropterygiinae in the morphological features by dorsal-fin origin near or before anus, anal-fin origin just behind anus (vs. dorsal and anal fins restricted to tail tip). That the species of *Scuticaria tigrina* and *Scuticaria marmorata* (previously grouped as “*Uropterygius*” *marmoratus*) are sister species within the

same genus is supported both by the morphological common feature of possessing thick intermuscular bones in caudal skeleton and by their close mitogenetic affinity. The results strongly suggest that so-called “*Uropterygius*” *marmoratus* is more logically to be placed in *Scuticaria* rather than in *Uropterygius*. The further detailed survey of fish group in another subfamily of morays may provide a deeper insight into the evolutionary history of this family which is still in progress.

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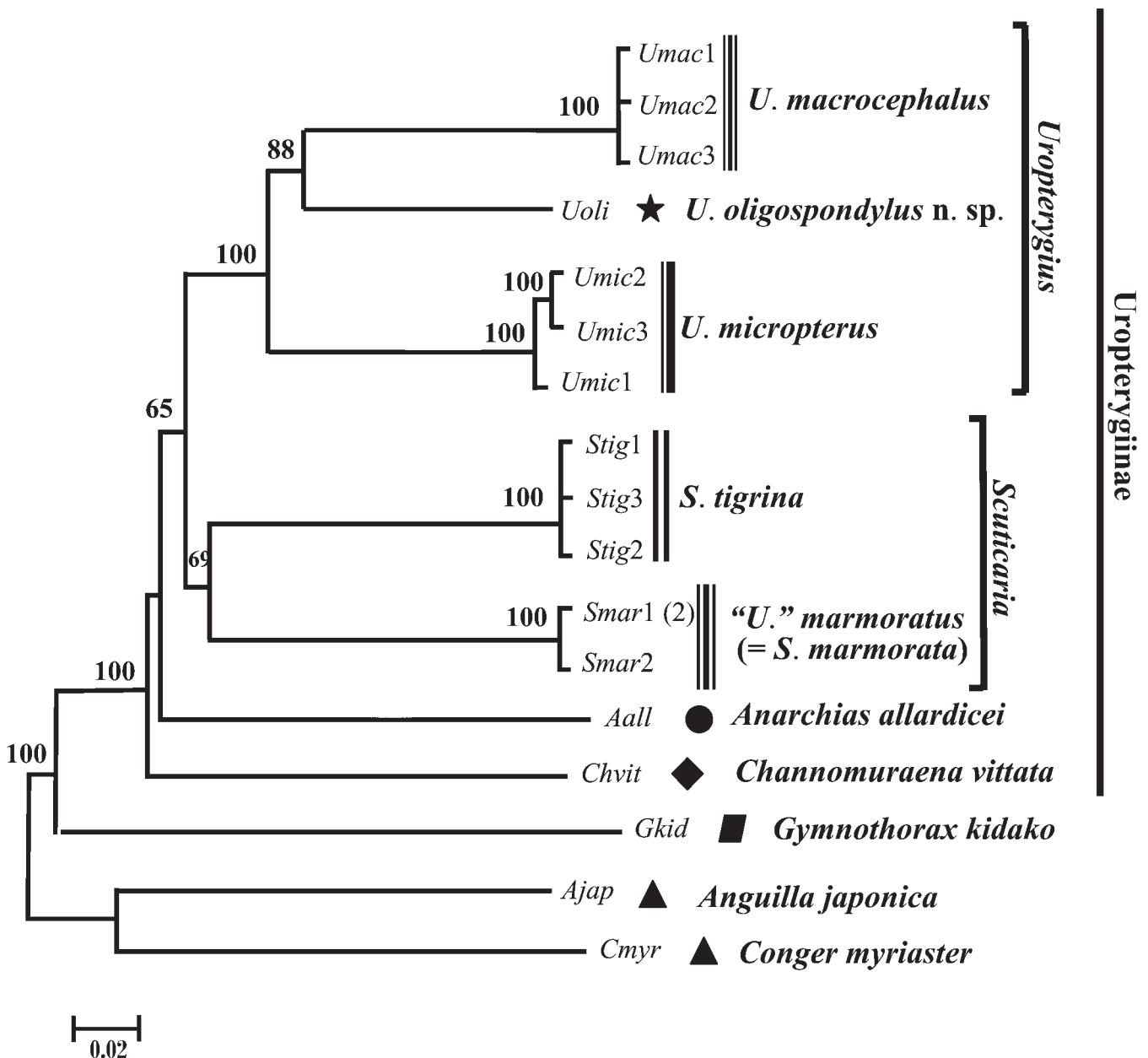


Fig. 6. Phylogenetic trees of mitochondrial ND5 for Uropterygiinae data from Taiwan. Neighbor-joining tree resulting from GTR+ I +G model distance. Numbers above the nodes indicate the bootstrap values for 1,000 replicates.

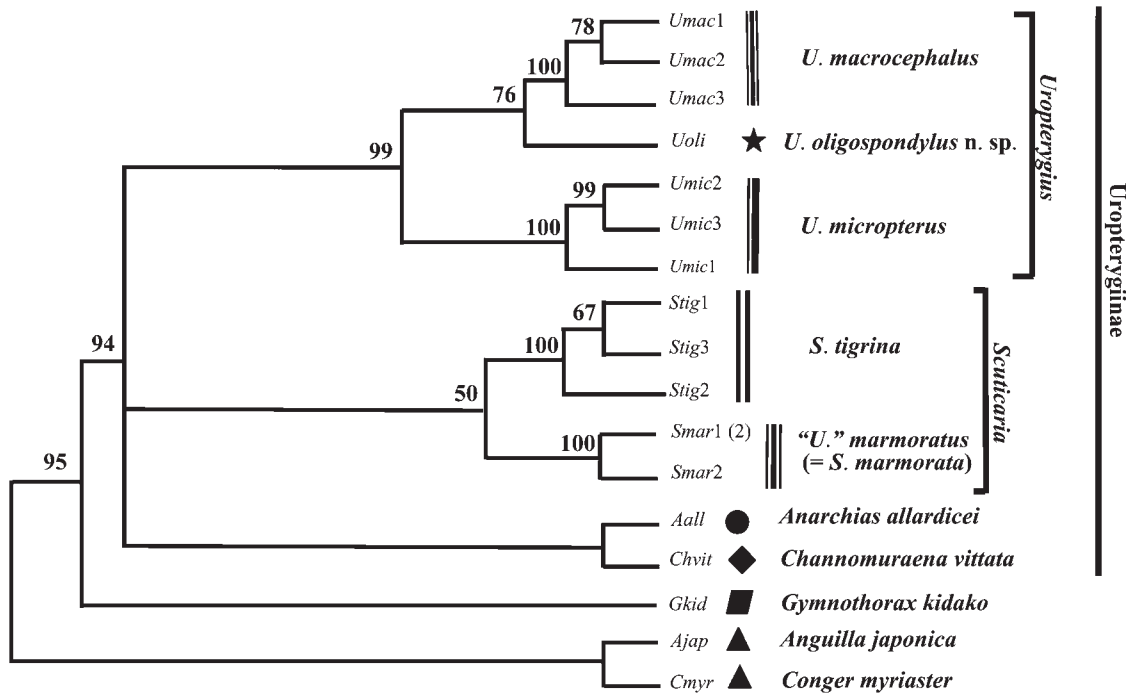


Fig. 7. Phylogenetic trees of mitochondrial ND5 for Uropterygiinae data from Taiwan. Maximum-Parsimony showing the consensus tree (CI = 0.588; RI = 0.671); bootstrap values (1,000 replicates) are indicated above branches.

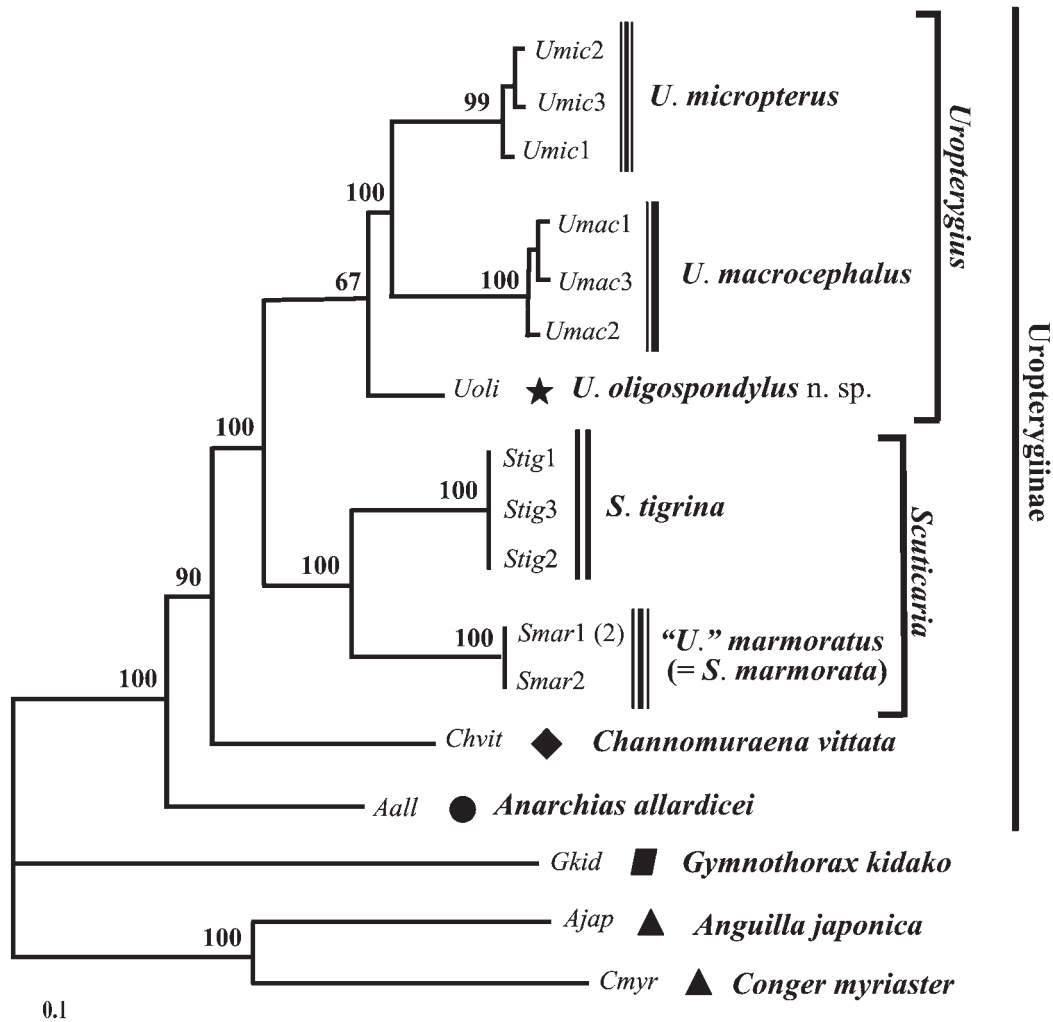


Fig. 8. Bayesian analyses of mitochondrial ND5 for Uropterygiinae data from Taiwan. GTR+ I +G model (values above the branch: posterior probability).

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THE RAFFLES BULLETIN OF ZOOLOGY 2008

Appendix I. The variable sites of ND5 sequence (length: 1,842 bp) from the species of Uropterygiinae in Taiwan.

	1111112	222333344	444445555	666667777	888889999	111111111	111111111	111111111	111111111
	6789234683	4570167902	3568901478	0136890258	1237890345	9235812456	7069256891	3780136902	5684780369
Umac1	TCCTTGTTCAT	TACTCTCACG	GGTGGTGTGG	TACATTACCC	AGACCAGACA	AGCAACCTAT	CGAAACAGCT	GCTTGTCTAG	CTATCTACAG
Umac2	.....	.....	.....	.....	.....	.....	.....	.....	.....
Umac3	.....	.....	.....	.....	.....	.....	.....	.....	.....
Umic1	...CAA....	..TA...CTA	.CCA..CC.A	.CT...A.A	.A..TCC..	.....C.C	T....CAA.	C....CT...	.CG..C....
Umic2	...CAA....	..TA...CTA	.CCA..CC.A	.CT...G..A	.A.A.TCC..	.....C.C	T....CAA.	C....CT...	.CG..C...A
Umic3	...CAA....	..TA...CTA	.CCA...C.A	.CT...G..A	.A..TCC..	.A.....C.C	T....CAA.	C....CT...	.CG..C...A
Uoli	.....A....	..TGA..C..	.CCA.CCC..	.TTG...A.A	GA.....CCA.	.....GC	.A...CA..	C..CA.T...	.CG.....G.
Smar1 (2)	.T...A.AG.	C....C.G.A	AT...CCC.A	.CTC.C...A	TAGTT.CC..	.A..AGG.C	.A.GG.CA.G	C...C..TC.C	T....G.G.
Smar2	.T...A.AG.	C....C.G.A	AT...CCC.A	.CTC.C...A	TAGTT.CC..	.A..AGG.C	.A.GG.CA.G	C...C..TC.C	T....G.G.
Stig1	CATC.ACA..	C..AAC.C.A	.CCA.CCCC.	CT.....TA	CAG...CT.G	.AA.G.TG.C	.A...A..A	C.C...A..	T....C..GA
Stig2	CATC.ACA..	C..AAC.C.A	.CCA.CCCC.	CT.....TA	CAG...CT.G	.AA.G.TG.C	.A...A..A	C.C...A..	T....C..GA
Stig3	CATC.ACA..	C..AAC.C.A	.CCA.CCCC.	CT.....TA	CAG...CT.G	.AA.G.TG.C	.A...A..A	C.C...A..	T....C..GA
Aall	.....A....	.C.AACTC.A	.AC.ACTCAA	.CT.....T	CAC...A.A.	C.AG..TA..	GAG..G...C	CTA.AC.AGA	.C.C.AGT.C
Chvit	.T.C.C...C	.....T..C	CAC.CCTCC.	.CTTC..TT	.T..GCG.G	.A..A.C.C	.C.GCTCA.A	C....C..G.	.CG.TCG.G.
	1111112222	222222222	222222222	222222222	223333333	333333333	333333333	333333333	444444444
	9999990011	1222233334	4445566677	7778888899	9900011122	3333444444	5555666677	7788899990	0011122223
	0257891736	9025801470	3695814703	6792345814	5703625818	0369012358	1247036925	8947813692	5614703692
Umac1	AGATCACTAA	ATCTATACTC	ACTCGTTACG	TACTGTATTC	TATCCACGGT	AACAAGCGAC	ACCGCGCTAC	TCCCTGGAAT	GCAGCCTGTA
Umac2	.....	.....	.....	.....	.....	.....	.....	.....	.....
Umac3	.....	.....	.....	.....	.....	.....	.....	.....	.....
Umic1	GAG.T..C..	G.TC..G.C.	T....CC..A	CG..C..C.CT	CT....TAA.	C.T...T...	.T.ATC....	C..TC....C	.TTA...A..
Umic2	GAG.T..C..	G.TC....C.	T....CC..A	CG..C..C.CT	CT.....A.	.T...T...	.T.ATC....	C..TC....C	.TTA..C...
Umic3	GAG.T..C..	G.TC....C.	T....CC..A	CG..C..C.CT	CT.....AA.	.T...T...	.T.ATC....	C..TC....C	.TTA...C...
Uoli	.A...T...T	.A...G...T	T...ACC...T	C..C..T...T	C.C...TAA.	C.T...G...	.TTA.C....	CT.TC.A.G.	A.CA...A..
Smar1 (2)	.A..AGTCGC	...C....C.	CT.TACC.TA	.T.ACC...T	...TAT.AA.	...GGC.T.T	.A.A.CTC.T	AT.T.AC..C	...A...A..
Smar2	.A..AGTCGC	...C....C.	CT.TACC.TA	.T.ACC...T	...TAT.AA.	...GGC.T.T	.A.A.CTC.T	AT.T.AC..C	...A...A..
Stig1	.A..A....C	G.A.G....T	T....CCG.A	.....CCC.	C.C.AC.AAG	C.T.GCTAC.	.ATATA....	ATG..AC...	C..ATTC.CG
Stig2	.A..A....C	G.A.G....T	T....CCG.A	.....CCC.	C.C.AC.AAG	C.T.GC.AC.	.ATATA....	ATG..AC...	C..ATTC.CG
Stig3	.A..A....C	G.A.G....T	T....CCG.A	.....CCC.	C.C.AC.AAG	C.T.GCTAC.	.ATATA....	ATG..AC...	C..ATTC.CG
Aall	.A.CTG.A..	GG.CCCCA.T	T....CC...A	A....T.CT	C....C.A..	.G..GAG...	T....AT..T	G.A.CAT..C	A.TC.TCAC.
Chvit	TA..AG.C.C	..TCC.G...	G.C.ACC..A	G..CACCCCT	CCC.T..AA.	...CA.T..	CT...CTCGT	A.G.CACC.C	..GA.TC.C.
	4444444444	4444444444	4445555555	5555555555	5555555555	5555555566	6666666666	6666666666	6666666666
	3344455556	6777778888	9990011112	2233334444	5556666677	8889999900	0011222233	3333444455	5666677788
	5814703695	8124570369	2584734690	2512470369	2581457836	2582457906	7958145701	3469235814	7036925814
Umac1	TTTCAGATCA	TCCGCATCAG	CCACGCTCCT	AGTATCCTAA	TTACTAAAAC	GCCCGCGGTA	CTACCAGACA	AACACTAAAG	AAGTACATA
Umac2	.....	.....	.....	.....	.....	.....	.....	.....	.....
Umac3	.....	.....	.....	.....	.....	.....	.....	.....	.....
Umic1	.C.G.AC..G	.TT.T...G.	...A..TTC	.A..C....	C.GT....A	A.T.AAT.C	A...T.T.G	....C.CCA	.GCC.C..C.
Umic2	.C.G.AC..G	.TT.T...G.	...A..TTC	.A..C....	C.GT....A	A.T.AAT.C	A...T.T.G	....C.CCA	.GCC.C..C.
Umic3	.C.G.AC..G	.TT.T...G.	...A..TTC	.A..C....	C.GT....A	A.T.AAT.C	A...T.T.G	....C.CCA	.GCC.C..C.
Uoli	C..G.ATC.	CT.A..C..	...A...C	...A..CT.C	C.G.....	A...AA..C	A..TTG...	.GTG...G.A	.A.TGT.CG
Smar1 (2)	C.C.G.ACA..	.T.A....GA	.AG.CTG..C	.AC.C.TG.C	C.T.C.....	.G.AA.CA.	A.....T.	.G.G.C.CTA	.A.T..T..
Smar2	C.C.G.ACA..	.T.A....GA	.AG.CTG..C	.AC.C.TA.C	C.T.C.....	.G.AA.CA.	A.....T.	.G.G.C.CTA	.A.T..T..
Stig1	CC.G..CAG.	.T..T.C...	.A..CTGATC	GA.GC...T	C..TCCGGG.	.A.AAT.CG	ACG..G..T	.G.G.CG.TC	..CA.GTC.G
Stig2	CC.G..CAG.	.T..T.C...	.A..CTGATC	GA.GC...T	C..TCCGGG.	.A.AAT.CG	ACG..G..T	.G.G.CG.TC	..CA.GTC.G
Stig3	CCG..CAG.	.T..T.C...	.A..CTGATC	GA.GC...T	C..TCCGGG.	.A.AAT.CG	ACG..G..T	.G.G.CG.TC	..CA.GTC.G
Aall	C..AGAG.T.	AT.A..CA.A	TA.TC.GTTC	.AC.C..GC.	C.CTC....	ATA.AAT.C	AC...G.CA	GG.GTCC..C	CG.CTTT.A
Chvit	.C.A.ACA..	C....G..GA	...CTGATC	GA.CA..ATG	CCCTCTTGG.	..ATAA.CA.	A..TT.A.AC	.G...CCCA	.TAC.TTCA.
	6666677777	7777777777	7777777777	7777888888	8888888888	8888888888	8888888888	8889999999	9999999999
	8999900111	2223334445	5667778888	9999000011	1122223333	3444445556	6666777788	9990001122	3344455566
	7036925147	0362581477	9251470679	2568145704	6903581234	7034692681	2457036958	1470692847	3925812470
Umac1	AACGTCATGC	CAAACCTGAC	ATCAGGTCGG	TCCTTACCCA	TAGCCCGACA	CCCGCCCTGC	TTCCGCATTG	TCCATTGATA	CACAACCAGG
Umac2	.....	.....	.....	.....	.....	.....	.....	.....	.....
Umac3	.....	.....	.....	.....	.....	.....	.....	.....	.....
Umic1	G.TA..CCA.	.....A....	.C..A.CA.A	.T..CC.G..	C....AGTT	...A.TACAA	.ATAA.GCCA	.TT..C..C.	ACTGGGT..A
Umic2	G.TA..CCA.	.....A....	.C..A.CA.A	.T..CC.G..	C....AGTT	...A.TACAA	.ATAA.GCCA	.TT..C..C.	ACTGGGT..A
Umic3	G.TA..CCA.	.....A....	.C..A.CA.A	.T..CC.G..	C....AGTT	...A.TACAG	.ATAA.GCCA	.TT..C..C.	ACTGGGT..A
Uoli	..TA...A..	.....T...T	...AA.G.A	CA.A.C.T..	.....A...	...ATT.C.A	GC.AAA...A	C.T.CC....	AC.G...GA.
Smar1 (2)	...A.T.AAT	AC...T.C.C	T.T...CTAC	CTTACTAT..	.GCG..A..C	T.TA.T.CAG	GC..A...A	..ACCCT.AC	A...A.G.A
Smar2	...A.T.AAT	AC...T.C.C	T.T...CTAC	CTTACTAT..	.GCG..A..C	T.TA.T.CAG	GC..A...A	..ACCCT.AC	A...A.G.A
Stig1	G..A..TA..	GC...TCAC.	TC.GACC..A	.T..CC.TT.	C.CGA..G.C	G.G..T.C.G	GG.TA..CCA	.TTCCC..A	A...A..AA
Stig2	G..A..TA..	GC...TCAC.	TC.GACC..A	.T..CC.TT.	C.CGA..G.C	G.G..T.C.G	GG.TA..CCA	.TTCCC..A	A...A..AA
Stig3	G..A..TA..	GC...TCAC.	TC.GACC..A	.T..CC.TT.	C.CGA..G.C	G.G..T.C.G	GG.TA..CCA	.TTCCC..A	A...A..AA
Aall	GT.ACACCA.	TC.G.TCA..	GCA.A.GAAT	.G.C.C..T.	A..ATT.G.C	...A.TTC.G	GCATA...T	..A.CC.G.G	A.T..A..A.
Chvit	.TTA..CA.G	GCC.TTG...	TCA.A..AAT	...AC.AG.C	...A..A...	.A.AA.TCA.	GA..AAC.CC	..AC.....C	AC...A.G..

Appendix I. continued.

	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111
Umac1	9999999999	9900000000	0000000000	0000000000	0011111111	1111111111	1111111111	2222222222	2222222222
Umac2	6667778888	9900011223	3344455555	6667778888	9900111122	2233445555	6677778890	0002223444	4555556666
Umic1	3692581470	6295847392	5814701469	2680147069	5814034602	5817360268	1403692510	3461480568	9145780369
Umic2	CTTCATACGA	TCTCCCTCA	CCTCATCTTC	CAGGTTAGCC	AAGCCCTTC	GCTACATATG	AAATGCCCCA	CATGACCAAA	CCCCGATCCT
Umic3	...T.....	.....G	.....	.....	.....	.....	.....	.....	.....
Uoli	TA.TG.G.A.	CTCTTT.C.G	T...GCTA..	.CAAC.GA..	GGA..A.C..	..CG..CG.A	GGTC...AC	T.CAC.AC.C	.TAT..C..C
Smar1(2)	TA.TG.G.A.	CTCTTT.C.G	T...GCTA.T	TCAAC.G...	GGA..A.C..	..CG..CG.A	GGTC...AC	T.CAC.AC.C	.TAT..C..C
Smar2	TA.TG.G.A.	CTCTTT.C.G	T...GCTA.T	TCAAC.GA..	GGA..A.C..	..CG..CG.A	GGTC...AC	T.CAC.AC.C	.TAT..C..C
Stig1	..C.C.T.A.	CTC...T.CT.	T...CTA..	.CAA.CG..	..A...C..	A...G..CA	..CCA.GTT.	T.CAC.TC.T	.T.TAG...C
Stig2	T.CA.C.TAT	CTC.....	..GTGAGAC.	.CAA.CG..A	GGA.TG.CCT	CT...CCCCA	CGT.ATATT.	.CCCC..C.T	.GT.A..G.C
Stig3	T.CA.C.TAT	CTC.....	..GTGAGAC.	.CAA.CG..A	GGA.TG.CCT	CT...CCCCA	CGT.ATATT.	.CCCC..C.T	.GT.A..G.C
Aall	GCC..CGTAC	C.C.T.....	TTA..GTA.T	TCA.C...TT	GC...A.C..	C.CG..CCCA	CGCCA...A.	.CGAC.ACGC	TA....ATG
Chvit	GCC..CGTAC	C.C.T.....	TTA..GTA.T	TCA.C...TT	GC...A.C..	C.CG..CCCA	CGCCA...A.	.CGAC.ACGC	TA....ATG
	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111
Umac1	2222222222	3333333333	3333333333	3333333333	3333333333	3333444444	4444444444	4444444444	4444444444
Umac2	7778899999	0000111222	2223333333	4444455555	6666666788	8899000000	1111122223	3344555556	6666777777
Umic1	0281403679	2568147036	7891235689	0147803679	1234568703	6928124578	0367925681	5739234581	4789012346
Umic2	TTTACCACAC	CCTATGAAAA	TGTTCCCAA	ACCCACACGA	CCGCACAACA	CCAACGAACG	ACCCTCTGTC	CCACGATCAA	GCCTGACCCA
Umic3	...TT..T..	.TGC..C...	.TC.A.A...	..T.....	..A..T.G.G	....AT.TA	...AT.T.A	...A..T.C	A.ACC...T.
Uoli	..C.C.T.T.	..G.CA...	.AC...AT..	G.....TAC	..A...C.T.	T...TAT...	.GTAT.T.AT	.....	..A...T.C
Smar1(2)	..C.C.T.T.	..G...GC.	CAC...A...	.TGT.TGT.C	A.A...CT.	T..T.ATGG.	.GAGT.TAA.	..TT....G	A.GCCG...C
Smar2	..C.C.T.T.	..G...GC.	CAC...A...	.TGT.TGT.C	A.A...CT.	T..T.ATGG.	.GAGT.TAA.	..TT....G	A.GCCG...C
Stig1	..C.C.TGT..	T.GG.AGGCG	CA...TA.GT	C..T.T...C	A.A..TG...	..C.ACGA.	G.GGT..AA.	..CT..C..C	A.A.C.G..C
Stig2	..C.C.TGT..	T.GG.AGGCG	CA...TA.GT	C..T.T...C	A.A..TG...	..C.ACGA.	G.GGT..AA.	..CT..C..C	A.A.C.G..C
Stig3	..C.C.TGT..	T.GG.AGGCG	CA...TA.GT	C..T.T...C	A.A..TG...	..C.ACGA.	G.GGT..AA.	..CT..C..C	A.A.C.G..C
Aall	CC.T...TG.	TTGTC...T	.CCC.TA...	G..TG..TAC	AAA.C..C..	....AT.T.	G.AA..A.A.	.GT.AGCT..	A.ACC..A..
Chvit	.CA..T.T.T	TTGCA.CCC.	.CCC.TAT.T	CATT.T...C	...TCT.G..	.AGC.AC...	.AAG.C..A.	AGC.A.C.G.	.AATT.G..
	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111
Umac1	4444444444	4455555555	5555555555	5555555555	5555555555	5555555555	6666666666	6666666666	6666666666
Umac2	7888888999	9900000011	1112223333	3334445555	5666666677	7777889999	0000111111	2222233333	4444444445
Umic1	9023589123	4701346925	6781470134	5692581278	9012368923	4568170367	2458124578	0367890259	0123457890
Umic2	AAATTACCTT	CTTACCATA	GTCCAACACG	ACTATAACAA	CCACCAACCA	CTCCCCATAT	CATCCGAATA	ATGACTCTAC	TCACCCGGTC
Umic3	.....G.	.....A	.....	.....	.....	.....	.....	.....G.	.....
Uoli	.C.GCC..AC	..C...G.T	..T..T..A	G.CC...A.G	.....	TC.T..G..C	..C.A..G.G	TCATTC.CTA	.T...T....
Smar1(2)	.C.G.G..AC	..A.TATCCC	A.A...TG.A	.TA.C...C	.AG..C.AT.	.C.AT..C.C	..TTACCA.	.CA..A..G	.A.GT..TC.
Smar2	.C.G.G..AC	..A.TATCCC	A.A...TG.A	.TA.C...C	.AG..C.AT.	.C.AT..C.C	..TTACCA.	.CA..A..G	.A.GT..TC.
Stig1	.C.GGT.AAC	TGA..AT..T	ACA.GGTGTA	.G.C...GC	..T...GT.	.A.AT.GCG.	A.CT.ACCGG	CCA.TG.C.A	.A...CACT
Stig2	.C.GGT.AAC	TGA..AT..T	ACA.GGTGTA	.G.C...GC	..T...GT.	.A.AT.GCG.	A.CT.ACCGG	CCA.TG.C.A	.A...CACT
Stig3	.C.GGT.AAC	TGA..AT..T	ACA.GGTGTA	.G.C...GC	..T...GT.	.A.AT.GCG.	A.CT.ACCGG	CCA.TG.C.A	.A...CACT
Aall	GCGG..TAA.	G.GGTAGGCT	C.A.G.AG.A	G.G.C.G..G	TT.TAGTAT.	.AAA..CCGC	A.CT.ACCG	CCA.TA.C.G	C.T..TAACT
Chvit	.CGG...GTC	TCA.TATC.T	T.AGCGGAA	CTAGCGG.G.	.....A.G	.A.T.T.C.G.	GT.T.A.GAG	CCCCTACCA	..G..T.ACT
	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111	1111111111
Umac1	6666666666	6666677777	7777777777	7777777777	7777777777	7777888888	8888888888	8888888888	8888888888
Umac2	5667777888	8999900011	1222222234	4445555666	6777788888	9999900011	1111122233	333334	7013925689
Umic1	3681567036	9235824767	9023456840	3690258146	7013925689	1247813623	5678945623	456782	5678945623
Umic2	TCTCACCCCA	CACCGATACC	TGCCTAGCGA	CGAACTCAAA	AATAGCCAG	CATCTCTCGC	CGTATCTAC	CCGACA	CCGACA
Umic3	.....G.	.....G.	.....	.....	.....	.....	.....	.....	.....
Uoli	.AC...A..	T..T.GG..A	..T..C...G	.AG..C.CG.	..CTAT..G.	..C..TGTA	T..C..G.C.	.A....	.A....
Smar1(2)	.AC...A..	T..T.GG..A	..T..G..A.	.AG..C.CG.	..CTAT..G.	..C..TGTA	T..C..G.C.	.A....	.A....
Smar2	.AC...A..	T..T.GG..A	..T..G..A.	.AG..C.CG.	..CTAT..G.	..C..TGTA	T..C..G.C.	.A....	.A....
Stig1	.ACT...AT.	.G..AGA...	C.T..T...G	.AG...T..	GCC.A...	....A.AA	T..C..G.C.	.A....	.A....
Stig2	AAC.G.TA..	TG..AGA...	A...CTTAT	TA..T.T..G	G.CTAAT..A	..C...ATAG	TATCGAGCC.	TAA..G	TATCGAGCC.
Stig3	AAC.G.TA..	TG..AGA...	A...CTTAT	TA..T.T..G	G.CTAAT..A	..C...ATAG	TATCGAGCC.	TAA..G	TATCGAGCC.
Aall	..C.G..A..	.G..AGA...	A.TT.TT.A	TA...C.G.	..CC.A...	..C..TA.AA	.AT.GAA.CT	.AGG..	.AGG..
Chvit	..C.G..A..	.G..AGA...	A.TT.TT.A	TA...C.G.	..CC.A...	..C..TA.AA	.AT.GAA.CT	.AGG..	.AGG..