

台灣鮭與太平洋鮭屬魚種間之粒線體 DNA、生長荷爾蒙基因的分子演化研究

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內政部營建署雪霸國家公園管理處保育研究報告

中華民國九十五年十二月

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摘 要

關鍵詞：台灣鮭魚、太平洋鮭屬、粒線體 DNA、生長荷爾蒙基因、遺傳標記

一、研究緣起

Oncorhynchus masou 為唯一僅分布於亞洲的太平洋鮭屬魚種，主要分佈在環日本海地區，包括日本全島、庫頁島、堪察加半島南部、東西伯利亞與韓國東部的溪流中與沿海。台灣則是唯一分佈該種魚類的亞熱帶國家，自 1917 年青木赳雄氏於梨山附近發現後，對全球魚類學界均造成震撼性的影響。然而由於台灣鮭魚在體型與外觀上與日本櫻鮭的陸封型 Yamame 十分接近，僅在一些細部特徵上有所不同。外表的差異甚難對不同亞種的櫻鮭甚至不同種的太平洋鮭屬仔魚做出確認，因此迄今仍有台灣鮭魚係日人自日本所引入之陸封型櫻鮭或是台灣鮭魚為數十年前大甲溪上游人工養殖而逃逸之虹鱒(fresh water from *Oncorhynchus mykiss*; Rainbow trout)等等臆測，吾人實有必要以分子遺傳學證據來證實台灣鮭魚確為台灣特有原生物種，以杜悠悠之口，並確立台灣鮭魚於魚類演化生態及生物地理學上的重要地位。

二、研究方法及過程

本研究利用分子選殖的技術分析台灣鮭魚種內的遺傳多樣性，並尋求可茲應用的分子標記作為往後親緣鑑定之用。另外亦與其他太平洋鮭魚屬(Genus *Oncorhynchus*)的魚種作種間遺傳多樣性的分析，藉分子演化的相關技術，來評斷台灣鮭魚的演化史。

三、重要發現

1. 我們已經成功的選殖並定序了太平洋鮭屬中的櫻鮭四大亞種——台灣鮭魚 (*Oncorhynchus masou formosanus*)、日本櫻鮭 (*Oncorhynchus masou masou*)、石川氏鮭魚 (*Oncorhynchus masou ishikawae*)、琵琶鮭

(*Oncorhynchus masou* subsp. ; Biwa salmon)及紅鮭(*Oncorhynchus nerka* ; sockeye salmon)、狗鮭(*Oncorhynchus keta* ; chum salmon)、銀鮭(*Oncorhynchus kisutch* ; coho salmo)的完整的粒線體 DNA。我們發現在 *Oncorhynchus masou* 各亞種中，台灣鮭魚、日本櫻鮭、琵琶鮭及石川氏鮭魚的粒線體長度均同為 16,652 bp。紅鮭的粒線體長度則為 16,658 bp、狗鮭與銀鮭的粒線體長度則均為 16,659bp。

2. 從粒線體 DNA 序列分析，台灣鮭魚絕非臆測之逃逸之人工養殖虹鱒。台灣鮭魚與虹鱒在太平洋鮭屬演化早期即分別獨立演化。
3. 台灣鮭魚確為台灣原生特有亞種，我們發現台灣鮭魚在 GH1 之 intron 3 (或 intron c) 的部分有一段 GCT 三個核酸鹼基對的缺失 (deletion)，而其他櫻鮭的亞種的相同位置均無此一現象。另外我們亦完成櫻鮭各亞種的完整粒線體 DNA 定序，分析其間遺傳距離 (genetic distance) 並推測其分歧分化時間 (divergence time) 後，我們推論日本琵琶鮭因琵琶湖陸封最早獨立演化，台灣鮭魚在更新世冰河期以台灣為避難所後，因冰河退卻及板塊活動於距今二十萬至四十萬年前即已陸封在台灣，而獨立演化成一特有亞種，台灣鮭魚的分化時間早於櫻鮭與石川氏鮭魚的分歧分化時間。因此，台灣鮭魚絕非近百年前才由日人所引入。
4. 我們從生長荷爾蒙基因片段與完整的粒線體 DNA 序列分析發現台灣鮭魚族群缺乏遺傳多樣性。雖然台灣鮭魚族群的基因多樣性非常低，我們仍然可以發現種內個體間的些微差異，這些變異代表著台灣鮭魚族群的基因體尚未到達完全均質化的地步。

四、主要建議事項

1. 台灣鮭魚確為台灣特有原生物種，其基因庫 (genome) 中保有較日本的櫻鮭與石川氏鮭魚原始的基因密碼，研究此一特有物種有助於釐清鮭科分子演化及生物地理學上的不少疑問。

2. 鮭魚為冷水性魚類，台灣鮭魚於冰河期避難台灣，並陸封於台灣而演化成台灣特有亞種，研究台灣鮭魚對氣候的適應(adaptation)與 fixation 的過程，可提供一個冷水性魚類對暖化的適應機制的模型。
3. 國內近已引入日本陸封型櫻鮭進行商業性的養殖，目前已知台灣鮭魚能與櫻鮭雜交並產出子代，因此應嚴加防範此一外來亞種入侵七家灣溪水域，以免因雜交優勢而導致原生特有亞種的滅絕。

ABSTRACT

Taiwan salmon (*Oncorhynchus masou formosanus*), an endangered landlocked subspecies of *O. masou* distributed at the southern limit of the distribution range of salmonids, had been found only in the stream of Chichiawan. In this study, the genetic differentiations from the other subspecies of *O. masou* and the divergence time of Taiwan salmon were estimated. To address this purpose, the complete mitochondrial genomes from four subspecies of *O. masou* namely *O. masou formosanus*, *O. masou ishikawae*, *O. masou masou* and Biwa salmon were determined. All the mitochondrial genomes consisting of 16,652 base pairs encode thirteen proteins, the 12S and 16 S ribosomal RNAs and 22 transfer RNAs. Their genes are ordered in the same way as most other vertebrates. Genetic distances were calculated by using Kimura's two parameter method. Our data showed that Biwa salmon may be the primitive form of the species *O. masou*, and the distance between Taiwan salmon and the other two subtaxa-- *O. masou ishikawae*, *O. masou masou* was only 0.37%. On the other hand, the genetic distance between *O. masou ishikawae* and *O. masou masou* was only 0.28%. These results indicate that Taiwan salmon diverged from the common ancestor of the *O. masou* complex before *O. masou ishikawae* and *O. masou masou* diverged. To adopt the evolutionary rate of base substitutions for mtDNA (0.9%/Mya) for the *O. masou* complex, we proposed that the divergence time of Taiwan salmon from the ancestor of the *O. masou* complex is estimated to be 400 thousand years ago. In the present study we also examined the genomic organization of growth hormone gene in the closely related species Formosan land-locked salmon. Sequence of the putative grow hormone genes were shared about 95% homology with the corresponding grow hormones from Masu salmon. In addition, the Y-linked type 2 growth hormone pseudogene was not observed in Taiwan salmon. Moreover, an unique tri-nucleotide

deleted (GCT) marker was only found in GH 1 intron 3 in Taiwan salmon.

Keywords: *Oncorhynchus masou formosanus*, genus *Oncorhynchus* , mitochondrial genome, growth hormone genes, phylogenetic studies

一、前言（緣起、前人研究）

鈎吻鮭屬(Genus *Oncorhynchus*)又稱為太平洋鮭魚屬(Pacific salmon)至少含有十個種，其中紅鮭(*Oncorhynchus nerka*; Sockeye salmon)、狗鮭(*Oncorhynchus keta*; Chum salmon)、銀鮭(*Oncorhynchus kisutch*; Coho salmon)、王鮭(*Oncorhynchus tshawytscha*; Chinook salmon)、粉紅鮭(*Oncorhynchus gorbuscha*; Pink salmon)多為遠洋降海迴游型，分布範圍均可橫跨北太平洋的東、西兩岸。這五種鮭魚各自具有顯著的型態與生態上的差異甚為容易分辨。虹鱒(*Oncorhynchus mykiss*; Rainbow trout)與切喉鱒(*Oncorhynchus clarki*)原本被歸類於大西洋鮭屬(Genus *Salmo*)自 1989 年後方由 Smith 與 Stearley 二氏根據其四十九項重要的型態特徵重新歸為太平洋鮭屬。虹鱒同時具有降海型與陸封型，其降海迴游型俗稱為鐵頭鮭(Steelhead salmon)，多分布於北起阿拉斯加南迄北加州的太平洋沿岸，僅少數分布於亞洲堪察加半島(Kamchatka peninsula)的厄霍次克海沿岸(Sea of Okhotsk)。切喉鱒則僅出現於北美洲太平洋沿岸，除分部於北起阿拉斯加南迄北加州沿岸外，亦有十四個陸封型亞種散佈於北美的淡水湖及溪流中。兩者在體色與外觀上亦有顯著特徵可供區別。研究鮭魚演化的學者推測上述鮭魚均由距今一千萬年前的共同祖先演化而來。櫻鮭(*Oncorhynchus masou*)為數量最少的降海型鮭魚，僅於亞洲發現，與多數太平洋鮭不同的是櫻鮭保存有較原始的、類似鱒(trout-like)的生活史：降海迴游型喪失遠洋迴游能力，陸封型不會在排卵後即死亡，甚至一生中具有多次產卵的能力。研究鮭魚演化的學者根據這樣的生活史認為櫻鮭可能是最早由太平洋鮭屬共同的祖先分化出來的一支。

櫻鮭的分佈區域僅限於環日本海地區，包括日本列島、庫頁島、堪察加半島南部、東西伯利亞與韓國東部的溪流中與沿海。多數分類學者認為櫻鮭共有四個亞種，Masu salom 即日人常稱的 Sakura masu 學名為 *O. masou masou*，廣佈於日本列島的日本海沿岸、朝鮮半島東岸與堪察加半島南部的海域及相關水系，為

數目最多的亞種，同時具有降海迴游及陸封型兩種不同的生活型態，其陸封型又稱為山女魚(Yamame 或 Yamabe)；石川氏鮭魚(Satsuki salmon; *O. Masou ishikwae*) 僅分布於日本本州南部的太平洋與瀨戶內海沿岸及相關水系，亦同時具有降海迴游型及陸封型，其陸封型稱為雨子(Amago)；陸封湖泊型的琵琶鮭(Biwa salmon) 僅存於日本本州中部滋賀縣的琵琶湖中，為一未定名亞種目前仍以 *O. masou* subsp. 稱之；台灣則是唯一分佈鮭魚的亞熱帶國家，台灣鮭魚(*O. masou formosanus*)所在的七家灣溪為全球鮭魚分佈最南限。

魚類的體型、外觀與生活史作為分類依據，在外觀上石川氏鮭魚的成魚與仔魚身體兩側均具有紅點，琵琶鮭仔魚具有紅點、成魚不具紅點，早期的分類學家以此特徵曾經誤將此二亞種歸於同一種，並命為 *O. rhododus*。台灣鮭魚則因體型、外觀上與陸封型櫻鮭相近，而被認為與櫻鮭同為 *O. masou*。不過根據許多分類學者的研究顯示，台灣鮭魚與日本櫻鮭仍具有一些不同之處，例如：不同的吻部形狀，較少的身體黑點數，較高的體高，較長的胸鰭和臀鰭，較多的脂鰭至側線鱗片數。台灣鮭魚的臀鰭軟條數，胸鰭軟條數及脊椎骨的數目，亦均顯著少於日本櫻鮭。此外，台灣鮭魚具有基鰓骨齒(basibranchial teeth；又名舌齒 hyoid teeth)；其鰓耙(gill-raker)近尖端兩側具有 2-3 個棘狀突起等等顯微特徵，讓魚類分類學家終將台灣鮭魚獨立成一特有亞種 *O. masou formosanus*。

二、目的

近年來由於分子生物技術的進展迅速，因此生物地理及演化等問題常根據不同個體遺傳物質之標誌（genetic marker）間的差異來分析。由於真核生物的基因體(genome)動輒由數十億個鹼基對所組成，不利於實驗上的操作，因此平均長度為15000-17000鹼基對的粒線體DNA（mtDNA）乃成為其中一有效的分析工具。粒線體DNA為一環形雙股密閉DNA，在脊椎動物中，每個細胞中約存在1000-10000個（multiple copies）。粒線體DNA的上的基因組成與結構均十分簡單，通常由37個基因組成，包含2個ribosomalRNA基因(rRNAs)，22個transfer RNA基因(tRNAs)，及13個攜帶著與有氧呼吸過程中電子傳遞鏈有關的酵素基因，另有一non-coding region，在脊椎動物中又名D-loop或control region(控制區域)。脊椎動物的粒線體基因體通常被描述為可自行複製(self-replication)、無介入子(intronless)、缺乏修補能力(non-repair)、無重組(non-recombination)和母系遺傳(maternal inheritance)等特性的簡單環形構造。由於複製過程缺乏校正修補能力，因此常有單一鹼基突變(point mutation)及長度突變(length mutation)的發生，許多研究均顯示粒線體DNA的突變速率約為核基因的5至10倍，由於沒有基因傳組發生，因此物種間粒線體DNA序列的差異適用於區別物種及族群間的分歧分化程度。特別是，它是透過母系遺傳，所以在追溯母系始祖時效果顯著。利用檢視粒線體DNA內發生突變速率可以算出物種的演化速率，已被廣泛運用在研究物種內的遺傳組成多樣性(genetic diversity)和族群遺傳結構(population genetic structure)，以瞭解物種內族群間的遺傳分化和基因交流程度。因此，粒線體基因庫的基因排列與序列多形性可提供極佳的遺傳標誌來定義族群、追蹤個體或具親源關係族群之演化歷史、或建立系統演化樹。

三、材料與方法

樣本採集：

在內政部營建署雪霸國家公園境內的大甲溪流域七家灣溪，撿取產卵後自然死亡的台灣鮭魚(*Oncorhynchus masou formosanus*)個體，以及用不傷害鮭魚生存的方式剪取其脂鰭及採集一些未受精卵來抽取 DNA 作為實驗的材料，並自日本東京海洋大學的大泉研究站取得*Oncorhynchus masou masou*(masu salmon)、*Oncorhynchus masou ishikawae*(Amago salmon)、琵琶鮭(Biwa salmon)的肌肉樣本，*Oncorhynchus nerka*、*Oncorhynchus kisutch*與 *Oncorhynchus keta*等肌肉樣本由高雄海洋科技大學水產養殖系黃貴民教授提供。肌肉、脂鰭組織均以70% 乙醇保存。

研究方法

粒線體(mtDNA)的定序及分析

1. DNA 萃取

- (1) 取微量離心管,加入1x digestion buffer (1%SDS, 1mg/ml DTT, 0.5mg/ml proteinase K, 10mM Tris-HCl pH 8.0, 2mM EDTA)與組織，置於55°C之恆溫槽反應隔夜。
- (2) 加入一倍體積5M LiCl與兩倍體積之chloroform/isoamyl alcohol萃取，搖盪30分鐘；以12.5k rpm離心,取上清液。
- (3) 在上清液加入兩倍體積的100%室溫酒精，混合均勻後，12.5k rpm 離心15分鐘，倒掉上清液，再以200 ul 75%酒精清洗DNA沈澱物，再以12.5k rpm 離心5分鐘，小心抽乾酒精，可見白色或透明DNA沈澱物黏附於管壁上，自然乾燥數小時，以去除殘餘酒精，最後加入50ul無菌水溶解DNA。產物的確定: 取1ul DNA溶液，1ul 6倍的染色溶液(loading dye)及4 ul TE buffer，放入0.8%

瓊脂凝膠(agarose gel)中，電泳槽中放入1倍TBE buffer，以100伏特電壓電泳約40分鐘後，將瓊脂凝膠放入200 ml去離子水中，並加入10 ul 溴化乙啶(EtBr 10mg/ml)，水平搖盪40分鐘，將染色液倒掉，加入200ml去離子水，脫去多餘的溴化乙啶，再以紫外光照射瓊脂凝膠，查看是否有DNA存在。

2. 以雙股DNA聚合酶連鎖反應大量增幅DNA

(1)引子的設計

自行設計引子:利用SequencherTM4.0輸入由NCBI上所查到已登錄的虹鱒(rainbow trout; *Oncorhynchus mykiss*)的完整粒線體DNA序列，剔除高變異性的區域，再利用FASTPCR就基因保守區域去做分析，找出最適當的17對primer，各預定放大的contig 間相互重疊(overlap)約200 bp，以利定序後的assemble作業如圖一。PCR所使用的primer 序列如表一。放大Growth hormone 基因的primer set 序列如表二。

(2)聚合酶鏈反應(polymerase chain reaction)

聚合反應時，反應液25ul中包括5 ul 10 倍反應緩衝溶液(50Mm KCl, 10 Mm Tris-HCl pH 8.3) ，200mM dNTP(即分別含有200mM dATP、dCTP、dGTP、dTTP)，並加上10pm所需增幅的一對引子，1ul 粗DNA為模板，4 units Supertherm 聚合酶，充分混勻後，將反應管放入溫度循環控制儀(thermal cycler)，先以94°C加熱5分鐘，再進行32-35次下述之流程:

- a.94°C 40秒，將雙股DNA變性解開(denaturing)。
- b.50°C 30秒，使互補雙股片段與引子鍊合(annealing)。
- c.72°C 1分30秒，此時聚合酶進行反應，再引子3'端延伸聚合反應(extension)。
- d.最後加熱 72°C 10 分鐘，讓反應不全的片段繼續複製完成。

(3)定序

PCR產物以核酸自動定序儀 (ABI PRISM 3730 DNA Sequencer) 定序。並以 Sequence Analyzer軟體Chromas進行Base Calling與文字檔輸出。

(4)建立 DNA 序列矩陣與基因樹之建構

將所得序列送往 GenBank 以 BlastN 程式與 GenBank 中已登錄的序列進行比對分析後，再利用 Vector NTI 9.0 版將各 contig 組合。排序後之序列先以 MEGA 3.1 版軟體比較序列間發生鹼基替代(substitution)的情形，列出序列中的變異位置(variable sites 或 mutation sites)，以鄰近連接法(neighbor joining, 簡稱 NJ)法、Minimal Evolution 法繪出各物種間的演化樹。以 Modeltest version 3.06 尋求最適合的演化計算模式再以 PAU Pversion 4.0 採用高度簡約原理(maximum parsimony, 簡稱 MP)、鄰近連接法，及貝葉氏導出式(Bayesian inference, 簡稱 BI)三種分析方式來進行分析，而演化樹的支持度以 bootstrap 值及後驗概率 (posterior probability) 來檢視。最大概率 (Maximum Likelihood) 法則以 <http://power.nhri.org.tw/power> 之 POWER version 1.0 版進行分析。遺傳距離矩陣採 Kimura 的 two-parameter 模式估算。

四、結果與討論

一、櫻鮭生長荷爾蒙基因分子演化研究

我們藉著 PCR 放大台灣鮭魚 GH gene 的片段，探尋台灣鮭魚是否存在有 GH- ψ ，並利用 DNA 定序分析台灣鮭魚與日本櫻鮭家族在 GH gene 間的差異，同時調查台灣鮭魚個體與個體間的種內差異 (diversity)。

我們發現：

1. 台灣鮭魚與虹鱒(rainbow trout ; *Oncorhynchus mykiss*)的 GH 1 基因之 intron 3 序列有極大的差異 (圖二)。虹鱒的幼魚和櫻鮭一樣體側帶有圓黑斑紋，乍看之下很難區分，利用此分子標記即可很容易的區分兩者之仔稚魚。此外虹鱒的染色體數目 (58~60) 和櫻鮭的染色體數目 (66) 相差 6 到 8 條染色體。
2. 台灣鮭魚(雌雄兩性)沒有如一些櫻鮭家族成員一樣有 pseudogene GH- ψ 的存在 (圖三)。台灣鮭魚無法以 pseudogene—GH- ψ 來判別鮭魚的性別。
3. 台灣鮭魚在 GH 1 之 intron 3 (或 intron c) 的部分有一段 GCT 三個核酸鹼基對的缺失 (deletion)，而其他櫻鮭家族的成員 (櫻鮭與石川氏鮭魚) 基因上均無此現象 (圖四)。台灣鮭魚是歷經數十萬到數百萬年演化後落地生根於台灣的物種，不可能是 100 年前日本人殖民佔領台灣時從日本拿日本櫻鮭來放流的。
4. 九尾台灣鮭魚的 GH 2 之 exon 5、intron 5 及 exon 6 序列的基因，同質性非常高，在 380 bp 中 homology 幾乎達 100%。僅有在 exon 6 部位有一個 A/G 的 heterozygotes (圖五)。顯示台灣鮭魚族群缺乏遺傳多樣性。

二、鮭科粒線體 DNA 分子演化研究

利用上述的 universal primer sets 我們已經成功的選殖並定序了太平洋鮭屬中的櫻鮭四大亞種——台灣鮭魚(*Oncorhynchus masou formosanus*)、日本櫻鮭(*Oncorhynchus masou masou*)、石川氏鮭魚(*Oncorhynchus masou ishikawae*)、琵琶鮭(*Oncorhynchus masou* subsp. ; Biwa salmon)及紅鮭(*Oncorhynchus nerka* ; sockeye salmon)、狗鮭(*Oncorhynchus keta* ; chum salmon)、銀鮭(*Oncorhynchus kisutch* ; coho salmo)的完整的粒線體 DNA。我們發現在 *Oncorhynchus masou* 各亞種中，台灣鮭魚、日本櫻鮭、琵琶鮭及石川氏鮭魚的粒線體長度均同為 16,652 bp。紅鮭的粒線體長度則為 16,658 bp、狗鮭與銀鮭的粒線體長度則均為 16,659bp(如圖六)。

一般而言太平洋鮭屬各物種之粒線體 DNA 的鹼基組成屬 AT-rich，以台灣鮭魚為例其粒線體 DNA 鹼基使用率分別為 A: 30.4%, C: 28.4%, G: 15.6% 與 T: 25.6%。粒線體 DNA 中各基因間的相對位置與多數脊椎動物的粒線體上的排列順序相同。分析太平洋鮭屬魚種的粒線體中的 protein-coding genes 後可見，不同魚種之間相同的 protein-coding genes 均具有很高的保存性(conservation)，不同魚種的同一基因的長度均相同，分別為 ND1 基因 975 bp、ND2 基因 1050 bp、CO1 基因 1551 bp、CO2 基因 691bp、ATP8 基因 168 bp、ATP6 基因 684 bp、CO3 基因 786 bp、ND3 基因 351bp、ND4L 基因 297bp、ND4 基因 1381 bp、ND5 基因 1839 bp、ND6 基因 522 bp、cytb 基因 1141 bp。可知太平洋鮭屬各物種的粒線體 DNA 沒有發生遺傳重組(genetic rearrangement)的現象，僅有少許的鹼基替換(nucleotide -substitution)。13 個 protein-coding genes 中有 12 個的 open reading frame 位於 H 股，僅 ND6 基因的 open reading frame 位於 L 股上。所有的 protein-coding gene 均以 methionine 起始，除了 CO1 以 GTG 作為起始密碼(start codon)外，其餘皆以 ATG 作為起始密碼。有八個基因的終止密碼(termination codon)為 TAA，ND1 與 ND3 則以 TAG 做為終止密碼，CO2、ND4 及 Cytb 的終

止密碼不完全，僅具有一個 T 鹼基，其完整的 TAA 終止密碼的建立有賴於 post-transcriptional polyadenylation 後所附加的兩個 A 鹼基。ATP 8/ATP 6 及 ND4L/ND4 基因間有重複序列(overlapping)，前者相互之間有 10 個鹼基對的重複，後者則有 7 個鹼基對的重複，ATP6 與 CO3 則首尾相連共用一個鹼基對。此外 ND5 與 ND6 所在位置為同屬一段雙股 DNA 的互補兩股(ND5 位於 H 股，ND6 位於 L 股)(表三)。櫻鮭四亞種粒線體基因的密碼使用狀況如表四。

此外太平洋鮭屬的粒線體中共攜帶有二十二個 tRNA 的基因，其中十四個位於粒線體的 H strand 上、八個位於 L strand 上，各個 tRNA 的長度均介於 64 至 75 bp 之間，因此每個 tRNA 均可以摺疊成首蓓葉型的二級結構，在所有的 tRNA 二級結構中 amino acid stem 均由 7 bp 所構成、TYC stem 由 5 bp 所構成、DHU stem 由 4 bp 所構成(tRNA-Ser(AGY)的 DHU stem 由 3 bp 構成)(圖七)。

太平洋鮭屬物種之 12S rRNA 基因的長度介於 946-947bp，而 16S rRNA 基因歧異性較大介於 1678-1755bp 之間，兩個 rRNA 基因位於 tRNA-Phe 與 tRNA-Leu(UUR)之間，其間間隔 tRNA-Val，許多關於物種的分子演化研究常採取 12SrRNA 與 16SrRNA 為之，但是就鮭科各物種 rRNA 基因長度相當且序列保存性甚高，以 12S rRNA 或 16SrRNA 並不適宜作為遺傳演化分析。

粒線體的控制區(control region)又稱為 D loop 位於 tRNA-Pro 與 tRNA-Phe 之間，各魚種間 D loop 長度由 946 bp-1005 bp 不等，櫻鮭各亞種的 D loop 長度均為 999bp，除非完整定序否則難以利用 D loop 長度區別太平洋鮭屬各物種。

此外太平洋鮭屬物種粒線體 L strand 的複製起始點 OriL 均位於 tRNA-Asn 與 tRNA-Cys 之間，由 33 個鹼基對所組成，這段 DNA 序列可摺疊成一個穩定的 stem-loop 二級結構，其中二十個鹼基對構成 stem 的部分，十三個鹼基對構

成 loop 的部分，與之相鄰的 tRNA-Cys 基因中也可以發現保存性甚高的 5'-GCCGG-3' 序列。

我們為了了解台灣鮭魚個體間是否仍有多樣性存在，因此完成了三個台灣鮭魚樣本的完整粒線體 DNA 定序，其一為雄性來自於第一、二號壩間(編號 Taiwan salmon 1)，其二分別為一公一母來自於七號壩之上，分析所得完整序列發現，來自於七號壩以上的兩個樣本其 16,652bp 序列完全一致(編號 Taiwan salmon 7)，但與來自於第一、二號壩間的樣本有十個鹼基對的變異。我們同樣取了來自於同一族群的日本的陸封型 Amago salmon 的兩個樣本(編號 Amago 1 及 Amago 5)做相同的分析，發現兩者間亦有十二個鹼基對的差異。分析台灣鮭魚與櫻鮭其他亞種間粒線體 DNA 間的鹼基對取代數目，則可發現台灣鮭魚與琵琶鮭有 142-144 個鹼基的差異，台灣鮭魚與櫻鮭及石川氏鮭魚則均同為 61 個鹼基對的不同(表五)。

利用完整的粒線體的序列以 Common whitefish(*Coregonus lavaretus*) 做為外群，使用鄰接法(Neighbor-Joining; NJ)、最小進化法(Minimum Evolution; ME)、最大簡約法(Maximum Parsimony; MP)和最大似然法(Maximum Likelihood; ML) 建構的演化樹分別如圖八、圖九、圖十以及圖十一所示。四者分析的結果雖然大致上相似，且多數的分枝 bootstrap 支持度都在 90 以上。其中，櫻鮭四亞種中琵琶鮭確為最早獨立演化的亞種，次為台灣鮭魚，櫻鮭與石川氏鮭魚雖然已經可以明確的分群，但是其間支持度的 bootstrap 值較低均僅超過 60%。同一亞種內的不同個體亦可透過此法歸為同一群。至於虹鱒(Rainbow trout; *Oncorhynchus mykiss*)與櫻鮭則清楚可見兩者在太平洋鮭屬分化的早期階段即以分道揚鑣。

四個演化樹中最大的差異在於 NJ、ME 與 MP 三種建構方式均把紅鮭(Sockeye salmon; *Oncorhynchus nerka*)與虹鱒置於同一分枝上，但是 ML 法則認為紅鮭與櫻

鮭屬於同一演化分枝。

以 Kimura's two-parameter genetic distance 法分析所有已知鮭科 (family *Salmonid*) 完整的粒線體 DNA 序列，所得的遺傳距離如表六。

Wilson 等人曾估計鮭科粒線體 DNA 鹼基對替換速率與分化時間約為 2%/每百萬年，若以此推估則台灣鮭魚與櫻鮭 (*Masu salmon*) 及石川氏 (*Amago salmon*) 遺傳距離相同都是 0.37%，則台灣鮭魚在大約二十萬年左右就無法與北方的同種鮭魚進行基因交流。然而以此方法推估則太平洋鮭屬與大西洋鮭屬間的分歧分化時間為 550 萬年前，顯然與化石證據不符。

Oohara 等人採用 Martin and Palumbi 兩氏所推估的粒線體 DNA 鹼基對替換速率與分化時間 0.5-0.9%/每百萬年，如此所計算出的分歧分化時間與目前所知的化石證據較為吻合 (根據化石證據推估太平洋鮭屬與大西洋鮭屬的分歧分化時間約為一千一百萬年前，*Sockeye salmon* 則出現於六百萬年之前)，因此我們採用 0.9%/每百萬年來推估鮭科各物種的分歧分化時間得到以下結論：

1. 太平洋鮭屬 (genus *Oncorhynchus*) 與大西洋鮭屬 (genus *Salmo*) 的分歧分化時間約距今一千二百萬年前。
2. 太平洋鮭屬的演化分為兩支進行，其中一支進入到東亞海域因冰河所形成的地理障礙而在東亞獨自演化成櫻鮭一種 (*Oncorhynchus masou*)，櫻鮭各亞種已失去遠洋迴游能力。另一支則陸續演化成目前縱橫太平洋兩岸的太平洋鮭魚屬各種。我們推測兩支的分歧分化時間為距今八百五十萬年前。
3. 琵琶鮭魚是櫻鮭所有亞種中最早分化出來的，他與台灣鮭魚的遺傳距離約為 0.8% 推估可能在距今一百萬年前即因琵琶湖陸封，而在琵琶湖中獨自演化。
4. 台灣鮭魚與櫻鮭 (*Masu salmon*) 及石川氏 (*Amago salmon*) 遺傳距離相同都是 0.37%，推測台灣鮭魚在大約四十萬年左右就無法與北方的同種鮭魚進行基

因交流, 這個時候大約是里斯冰河期結束的時代。因此, 台灣鮭魚絕非近百年前才由日人所引入。

5. 兩個日本櫻鮭間的遺傳距離為 0.27% 推測兩者應該在距今三十餘萬年前開始分歧。

五、建議事項

1. 台灣鮭魚確為台灣特有原生物種，其基因庫(genome)中保有較日本的櫻鮭與石川氏鮭魚原始的基因密碼，研究此一特有物種有助於釐清鮭科分子演化及生物地理學上的不少疑問。
2. 必須建立台灣鮭魚遺傳多樣性的管理，在復育過程中應注意基因譜系的追蹤，並做計劃性的配對以維持有效族群數量，維持或減緩目前遺傳多樣性的消失速度。
3. 國內近已引入日本陸封型櫻鮭進行商業性的養殖，目前已知台灣鮭魚能與櫻鮭雜交並產出子代，因此應嚴加防範此一外來亞種入侵七家灣溪水域，以免因雜交優勢而導致原生特有亞種的滅絕。
4. 鮭魚為冷水性魚類，台灣鮭魚於冰河期避難台灣，並陸封於台灣而演化成台灣特有亞種，研究台灣鮭魚對氣候的適應(adaptation)與 fixation 的過程，可提供一個冷水性魚類對暖化的適應機制的模型。

誌謝

本計劃得以順利完成首先要感謝雪霸國家公園管理處 林前處長永發、 林處長青、 彭副處長茂雄的支持與鼓勵，沒有各位長官的提攜與厚愛，此計劃將無法推動進行，在此謹表由衷的敬佩與感謝。在執行過程中更應感謝保育課 徐課長、解說課 楊課長兩位所提供寶貴的建議，廖林彥君熱心提供樣本、于淑芬小姐及雪霸國家公園管理處保育課、秘書室及會計室各位同仁的全力支援，也使我們深銘五內。另外台灣海洋大學郭金泉教授的協助、指導與教誨更讓我由衷感謝。此外高雄醫學大學張學偉教授、高雄海洋科技大學黃貴民教授、農委會特有生物保育中心蔡奇立研究員、中華醫事學院陳善夫老師、波士頓大學陳聖賢先生及加州大學洛杉磯分校陳琳惠小姐在實驗過程、數據分析及樣本收集上的協助，在此一併致謝。

最後感謝中華醫事學院 程董事長義福與 林校長壽宏，在兩位的支持與呵護下，讓本研究能夠盡情揮灑。

本研究若有疏漏、過失，則是本人才疏學淺，尚望不吝指教。

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七、附錄：

一、台灣鮭魚粒線體 DNA 完整序列

LOCUS DQ858456 16652 bp DNA circular VRT 20-JUL-2006

DEFINITION *Oncorhynchus masou formosanus* mitochondrion, complete genome.

ACCESSION DQ858456

VERSION DQ858456

KEYWORDS .

SOURCE mitochondrion *Oncorhynchus masou formosanus* (Taiwan salmon)

ORGANISM *Oncorhynchus masou formosanus*
Eukaryota; Metazoa; Chordata; Craniata; Vertebrata; Euteleostomi;
Actinopterygii; Neopterygii; Teleostei; Euteleostei;
Protacanthopterygii; Salmoniformes; Salmonidae; *Oncorhynchus*.

REFERENCE 1 (bases 1 to 16652)

AUTHORS Chang, H.-W., Chung, Y.H., Gwo, J.C., Lin, Y.F., Liao, L.Y., Chang, W.C.
and Chou, Y.C.

TITLE The complete mitochondrial genome of Taiwan salmon (*Oncorhynchus masou formosanus*)

JOURNAL Unpublished

REFERENCE 2 (bases 1 to 16652)

AUTHORS Chang, H.-W., Chung, Y.H., Gwo, J.C., Lin, Y.F., Liao, L.Y., Chang, W.C.
and Chou, Y.C.

TITLE Direct Submission

JOURNAL Submitted (18-JUL-2006) Institute of Biotechnology, Chung Hwa
College of Medical Technology, 89, Wen Hwa 1st St., Jente, Tainan
717, Taiwan

FEATURES Location/Qualifiers

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/organelle="mitochondrion"
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 CDS 5026..6075
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 FEKWSTMMLEDA"

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gene 8944..9111
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CDS 9102..9785
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QALTLTILLGFYFTFLQGMEYYEAPFTIADGVYGSTFFVATGFHGLHVI IGSTFLAVC
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ELASLTSKQFKTTPNLITHNFSNMLGFFPAI IHRLAPKLNLT LGQAIASQMVDTWFE
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二、琵琶鮭魚粒線體 DNA 完整序列

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DEFINITION *Oncorhynchus masou* 'Biwa' mitochondrion, complete genome.

ACCESSION EF105342

VERSION EF105342 GI:117957320

KEYWORDS .

SOURCE mitochondrion *Oncorhynchus masou* 'Biwa'

ORGANISM *Oncorhynchus masou* 'Biwa'

Eukaryota; Metazoa; Chordata; Craniata; Vertebrata; Euteleostomi;
Actinopterygii; Neopterygii; Teleostei; Euteleostei;
Protacanthopterygii; Salmoniformes; Salmonidae; *Oncorhynchus*.

REFERENCE 1 (bases 1 to 16652)

AUTHORS Hsiah, C. C., Gwo, J.-C., Ohta, H. and Chou, Y. C.

TITLE The phylogenetic relationship among the four subspecies of
Oncorhynchus masou

JOURNAL Unpublished

REFERENCE 2 (bases 1 to 16652)

AUTHORS Hsiah, C. C., Gwo, J.-C., Ohta, H. and Chou, Y. C.

TITLE Direct Submission

JOURNAL Submitted (06-NOV-2006) Department of Medical Technology, Chung Hwa
College of Medical Technology, 89, Wen Hwa 1st St., Jente, Tainan
717, Taiwan

FEATURES Location/Qualifiers

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 /protein_id="ABK59099"
 /db_xref="GI:117957322"
 /translation="MNPYVLTILISSLGLGTVLTFASSHWLLAWMGLEINTLAIPI
 AQQHHPRAIEATTKYFLTQATAAMILFASTTNAWLMGEWEIHQLSHPLATTTAMLAL
 ALKLG LAPVHFWLPEVLQGLELTTGLILSTWQKLAPFALMIQVAPSIDSSLLIAIGLM

STLVGWGGLNQTLRKLAYSSIAHLGWMVLIQFAPSLTLLSLSLYIIMTSSAFLT
 LKTNNSLTINALATSWTKSPTLAALTALVLLSLGGLPPLSGFMPKWLILQELTKQELP
 LIATLAAMTALLSLFYLRCLYALTLTIYPNTLTATAPWRLNFTMFSPLSIVTILAL
 GLLPLTPAVSAMLTL"

tRNA 6078..6147
 /product="tRNA-Trp"

tRNA complement(6150..6218)
 /product="tRNA-Ala"

tRNA complement(6220..6292)
 /product="tRNA-Asn"

rep_origin complement(6293..6325)
 /note="OriL"

tRNA complement(6326..6392)
 /product="tRNA-Cys"

tRNA complement(6393..6463)
 /product="tRNA-Tyr"

gene 6465..8015
 /gene="C01"

CDS 6465..8015
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 /codon_start=1
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 /product="cytochrome c oxidase subunit 1"
 /protein_id="ABK59100"
 /db_xref="GI:117957323"
 /translation="MAITRWFSTNHKDIGTLYLVFGAWAGMVGTAALLIRAELSQP
 GALLGDDQIYNVIVTAHAFVMIFFMVPMIGGFGNWLIPLMIGAPDMAFPRMNNMSF
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 AINFITTIINMKPPAISQYQTPLFVWAVLVTAVLLLLSLPVLAAAGITMLLTDRLNNT
 FFDPAAGGDPILYQHLFWFFGHPEVYILILPGFGMISHIVAYYSGKKEPFGYMGVWA
 MMAIGLLGFIVWAHMFVGMVDVTRAYFTSATMIIAIPGKVFVSWLATLHGGSIKW
 ETPLLWALGFIFLFTVGGTGVIVLANSGLDIVLHDTYYVVAHFHYVLSMGAVFAIMGA
 FVHWFPFTGYTLHSTWTKIHFGIMFIGVNLTFPQHFLGLAGMPRRYSDYPPDAYTLW
 NTVSSIGSLVSLVAVIMFLFILWEAFAAKREVASIELTSTNVEWLRGCCPPPYHTFEFP
 AFVQVQAN"

tRNA complement(8016..8086)
 /product="tRNA-Ser"

tRNA 8090..8163

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        /product="tRNA-Asp"
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        /gene="CO2"
CDS       8178..8868
        /gene="CO2"
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        residues to the mRNA"
        /codon_start=1
        /transl_except=(pos:8868,aa:TERM)
        /transl_table=2
        /product="cytochrome c oxidase subunit 2"
        /protein_id="ABK59101"
        /db_xref="GI:117957324"
        /translation="MAHPSQLGFQDAASPVMEEELHFHDHALMIVLLISTLVLYIIVA
        MVSTKLTNKYILDSQEIEIVWTVLPAVILILIALPSLRILYLMDEINDPHLTIKAMGH
        QWYWSYEYTDYEDLGFDSYMPVPTQDLVPGQFRLETDHRMVVPVESPIRILVSAEDVL
        HSWAVPSLGVKMDAVPGRLNQTAFIASRPGVFFYGCSEICGANHSFMPIVVEAVPLEH
        FEKWSTMMLEDA"
tRNA      8869..8942
        /product="tRNA-Lys"
gene      8944..9111
        /gene="ATP8"
CDS       8944..9111
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        /codon_start=1
        /transl_table=2
        /product="ATP synthase F0 subunit 8"
        /protein_id="ABK59102"
        /db_xref="GI:117957325"
        /translation="MPQLNPAPWFVAILVFSWLVFVLTIVIPKVLGHTFTNEPTSQSTEK
        AKPEPWNWPWH"
gene      9102..9785
        /gene="ATP6"
CDS       9102..9785
        /gene="ATP6"
        /codon_start=1
        /transl_table=2
        /product="ATP synthase F0 subunit 6"

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LTANLTAGHLLIQLIATAAFVLLPLMPTVAILTSIVLFLLLTLEIAVAMIQAYVFVLL
LSLYLQENV"
gene      9785..10570
          /gene="C03"
CDS       9785..10570
          /gene="C03"
          /codon_start=1
          /transl_table=2
          /product="cytochrome c oxidase subunit 3"
          /protein_id="ABK59104"
          /db_xref="GI:117957327"
          /translation="MAHQAHAYHMVDPSPWPLTGAIAALLTSGTAVWVHFHSLTLLT
LGNVLLLLTMYQWWRDI IREGTFQGHHTPPVQKGLRYGMILFITSEVFFFLGFFWAFY
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QALTLTILLGFYFTFLQGMEYYEAPFTIADGVYGSTFFVATGFHGLHVIIGSTFLAVC
LLRQVQYHFTSEHHFGFEAAAWYWHFVDVVWVFLYVSIYWWS"
tRNA      10570..10639
          /product="tRNA-Gly"
gene      10640..10990
          /gene="ND3"
CDS       10640..10990
          /gene="ND3"
          /note="TAA stop codon is completed by the addition of 3' A
residues to the mRNA"
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          /transl_table=2
          /product="NADH dehydrogenase subunit 3"
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          /db_xref="GI:117957328"
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LIYEWTOGGLEWAE"
tRNA      10990..11058

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gene     11059..11355
        /gene="ND4L"
CDS     11059..11355
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        /transl_table=2
        /product="NADH dehydrogenase subunit 4L"
        /protein_id="ABK59106"
        /db_xref="GI:117957329"
        /translation="MTPVHFSFTSAFILGLMGLAFHRTHLLSALLCLEGMMLSLFIAL
SLWALQMEATGYSVAPMLLLAFSACEASAGLALLVATARTHGTDHLQSLNLLQC"
gene     11349..12729
        /gene="ND4"
CDS     11349..12729
        /gene="ND4"
        /note="TAA stop codon is completed by the addition of 3' A
residues to the mRNA"
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        /protein_id="ABK59107"
        /db_xref="GI:117957330"
        /translation="MLKILIPTLMLFPTIWLSPAKWLWTTTIAQSLIIALASLSWLKW
SSETGWSSSNLYLATDPLSTPLLVLTCWLLPLMILANQNHSPEPLNRQRAYISLLVS
LQTFVLVAFGATEIIMFYIMFEATLLPTLIIITRWGNQTERLNAGTYFLFYTLAGSLP
LLVALLMQNDSGTL SMFTLQYMQPVHLLTWGDKLWAAACLLAFLVKMPLYGVHLWLP
KAHVEAPIAGSMILAAVLLKLGGYGMMRMVVLDPLTKELAYPFI VLALWGIIMTGSII
CLRQTDLKSIIAYSSVGHMGLVAGGILIQTPWGFSGAII LMI AHGLASSALFCLANTS
YERTHSRTMLLARGMQMILPLMTTWWF MASLANLALPPLPNLMGELMIITSMFNWSYW
TLILTGLGTLITASYSLYFLMTQRGPLPSHIIALEPHTREHLLIMLHLIPIVLLIL
KPELMWGWCF"
tRNA     12730..12798
        /product="tRNA-His"
tRNA     12799..12867
        /product="tRNA-Ser"
tRNA     12869..12941

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        /product="tRNA-Leu"
gene      12942..14780
        /gene="ND5"
CDS       12942..14780
        /gene="ND5"
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        /product="NADH dehydrogenase subunit 5"
        /protein_id="ABK59108"
        /db_xref="GI:117957331"
        /translation="MHP TTLILSSLLMIFALLIYPLITLTP TLQHKNWALTHVKTA
IKMAFLVSLPLFIFLDQGTETIVTNWQWMMTTTTFDINLSFKFDHYSIIFTPIALYVT
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GWWHGRADANTAAMQAVIYNRVGDIGLILSMAWFATNLNSWEIQQMFASSKELDLTLP
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QTALTTC LCLGALTTLFTATCALTQNDIKKIVAFSTSSQLGLMMVTIGLNQPQLAF LH
ICTHAFKAMFLFCSGSI IHSLNDEQDIRKMGGMHNLTPFTSSCLTIGSLALTGTPFL
AGFFSKDAIIEALNTSHLNAWALTLTLLATSFTAIYSLRVIFFVSMGHPRPTMTPIN
ENNSSVINPIKRLAWSIVAGLLITSNFLPSNTPVMTMPHLKLAALLVTILGLI IAL
ELASLTSKQFKTTPNLI THNFSNMLGFFPAI IHRLTPKLNLT LGQAIASQMVDQTWFE
KVGPKGVISTHLPVMTTTSNIQQGMIKTYLTLFFFSTTLAVLLTLT"
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        /gene="ND6"
CDS       complement(14777..15298)
        /gene="ND6"
        /codon_start=1
        /transl_table=2
        /product="NADH dehydrogenase subunit 6"
        /protein_id="ABK59109"
        /db_xref="GI:117957332"
        /translation="MTYLVSLFLLGLVGLVAVASNPAPYFAALGLVVAAGVCGV LV
GHGGSFSLVLF LIYLGMLVVFAYSAALAAEPFPESWGDRSVLGYVMVYMGVVLVA
GLFWGGWYETSWVAVDEFKEFSVLRGDTSGVGLMYSYGGGMLIVCAWVLLLTLFVVLE
LTRGLGRGALRAV"
tRNA      complement(15299..15367)
        /product="tRNA-Glu"
tRNA      complement(15299..15366)
        /product="tRNA-Glu"

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gene      15371..16511
          /gene="cytb"
CDS       15371..16511
          /gene="cytb"
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          residues to the mRNA"
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          /product="cytochrome b"
          /protein_id="ABK59110"
          /db_xref="GI:117957333"
          /translation="MANLRKTHPLLKIANDALVDLPTPSNISVWWNFGSLLGLCLATQ
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          YYGSYLYKETWNIQVLLLLTMMTAFVGYVLPWGQMSFWGATVITNLLSAVPYVGNAL
          VQWIWGGFSVDNATLTRFFAFHFLFPFVITAAAILHLLFLHETGSNNPAGINSDADKI
          SFHPYFSYKDLLGFAAMLLCLTSLALFAPNLLGDPDNFTPANPLVTPPHIKPEWYFLF
          AYAILRSIPNKLGGVLALLFSILVLMVVPILHTSKQRGLTFRPLTQFLFWALVADMLI
          LIWIGGMPVEHPFIIIGQIASVIYFTIFLVLSPLAGWAENKALQWA"
tRNA      16512..16583
          /product="tRNA-Thr"
tRNA      complement(16583..16652)
          /product="tRNA-Pro"
BASE COUNT  4762 a  4679 c  2740 g  4471 t

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ORIGIN

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181  ttacattaag caaaacacgt gataataacc aactaagttg ttttaaactg attaattgct
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三、櫻鮭粒線體 DNA 完整序列

LOCUS DQ864465 16652 bp DNA circular VRT 25-JUL-2006

DEFINITION *Oncorhynchus masou masou* mitochondrion, complete genome.

ACCESSION DQ864465

VERSION DQ864465

KEYWORDS .

SOURCE mitochondrion *Oncorhynchus masou masou*

ORGANISM *Oncorhynchus masou masou*
Eukaryota; Metazoa; Chordata; Craniata; Vertebrata; Euteleostomi;
Actinopterygii; Neopterygii; Teleostei; Euteleostei;
Protacanthopterygii; Salmoniformes; Salmonidae; *Oncorhynchus*.

REFERENCE 1 (bases 1 to 16652)

AUTHORS Chang, H.-W., Chung, Y.H., Gwo, J.C., Lin, Y.F., Liao, L.Y., Chiang, J.H.
and Chou, Y.C.

TITLE The complete mitochondrial genome of *Oncorhynchus masou masou*

JOURNAL Unpublished

REFERENCE 2 (bases 1 to 16652)

AUTHORS Chang, H.-W., Chung, Y.H., Gwo, J.C., Lin, Y.F., Liao, L.Y., Chiang, J.H.
and Chou, Y.C.

TITLE Direct Submission

JOURNAL Submitted (22-JUL-2006) Institute of Biotechnology, Chung Hwa
College of Medical Technology, 89, Wen Hwa 1st St., Jente, Tainan
717, Taiwan

FEATURES Location/Qualifiers

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//

一、石川氏鮭魚粒線體 DNA 完整序列

LOCUS DQ864464 16652 bp DNA circular VRT 25-JUL-2006

DEFINITION *Oncorhynchus masou ishikawae* mitochondrion, complete genome.

ACCESSION DQ864464

VERSION DQ864464

KEYWORDS .

SOURCE mitochondrion *Oncorhynchus masou ishikawae* (Ishikawa's cherry salmon)

ORGANISM *Oncorhynchus masou ishikawae*
Eukaryota; Metazoa; Chordata; Craniata; Vertebrata; Euteleostomi;
Actinopterygii; Neopterygii; Teleostei; Euteleostei;
Protacanthopterygii; Salmoniformes; Salmonidae; *Oncorhynchus*.

REFERENCE 1 (bases 1 to 16652)

AUTHORS Chang, H.-W., Chung, Y.H., Gwo, J.C., Lin, Y.F., Liao, L.Y., Chang, W.C. and Chou, Y.C.

TITLE The complete mitochondrial genome of *Oncorhynchus masou ishikawae*

JOURNAL Unpublished

REFERENCE 2 (bases 1 to 16652)

AUTHORS Chang, H.-W., Chung, Y.H., Gwo, J.C., Lin, Y.F., Liao, L.Y., Chang, W.C. and Chou, Y.C.

TITLE Direct Submission

JOURNAL Submitted (22-JUL-2006) Institute of Biotechnology, Chung Hwa College of Medical Technology, 89, Wen Hwa 1st St., Jente, Tainan 717, Taiwan

FEATURES Location/Qualifiers

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tRNA 10990..11058
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gene 11059..11355
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CDS 11059..11355
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15061 ctgaaaagg ctacgagcc aaagccgctg aataagcaaa taccacaagt attccccca
15121 agtaaatcaa aaacgtacc aaagacaaga aagaccccc gtgaccacc aaaacaccac
15181 aaccacacc cgtctctaca actaaaccta aagcagcaaa ataaggtgca ggattagatg
15241 caacagctac aagccctaaa accagccta aaagaaataa agacacaaga taagcataa
15301 ttctgtctg gactctaacc gaaactaatg acttgaaaa ccaccgtgtt tattcaacta
15361 caagaacctc atggccaacc tccgaaaaac caccacctc ctaaaaatcg ctaatgacgc

15421 actagtcgat ctaccaacac catccaacat ctccgtctga tgaactttg gctcactttt
15481 aggccatgt ctagccaccc aaattcttac cggactcttc ttagccatgc actacacctc
15541 agatatttca acagcttttt cctctgtctg ccacatctgc cgagacgtta gttacggctg
15601 acttattcga aacatccatg ccaacggagc atctttcttt tttatttga tttatataca
15661 tatgcccg ggactttatt atggctcata cctttacaaa gaaacctgaa atatcggagt
15721 tgtactttta ctctcacta taatgactgc attcgtaggt tacgtccttc catgaggaca
15781 aatatccttc tgaggagcca ctgtcattac aaacctcctc tccgctgtcc catacgttgg
15841 aaacgccctt gtacaatgaa tctgaggcgg gttctctgtc gacaacgcca ctctgacacg
15901 atttttgcc tttcacttct tattcccttt cgtcattaca gctgctgcaa tcctccacct
15961 tctatttctt catgaaacag ggtcaaataa cccagcagga attaactccg atgctgataa
16021 aatctcgttc cacccttact tctctacaa agatctccta gggttcgag ctatacttct
16081 ctgtetaaca tccttagccc tttttgcacc aaatctccta ggagacccc acaattttac
16141 acccgcaac cctctagtta cccacccca catcaaacc gaatgatatt tcctattcgc
16201 ttacgcaatc ctacgateta tcccacaaca gctaggaggg gtactcgcctc tttattttc
16261 aatccttgtt cttatagttg ttcctatctt acacacttcc aaacaacggg gactaacctt
16321 tcgaccactg acccaattct tattctgagc cttagtagca gatatactta tcctcacctg
16381 aatcggaggc ataccgtag aacaccatt cattatcctc ggccaaattg cctctgtaat
16441 ctacttcacc atcttctag ttctctccc cttagctggc tgggccgaaa ataaagcctt
16501 ccaatgagcc tgcctagta gctcagcgc agagcgcgg tcttghtaat cggaagtcgg
16561 aggttaaac cctccctagt gctcagagag aggagatttt aactcccacc cttactccc
16621 aaagctaaga ttctaaatta aactactctc tg

//

表一、PCR放大櫻花鉤吻鮭粒線體DNA所使用的primer set 序列

primer	sequence
AF	5' TAACACGGGCTCCGTCTTTAC3'
AR	5' TTCAAAGGAGCTGTACCTCC3'
BF	5' CTGTTAAACCCCTAAACCAGG3'
BR	5' AGTCAGATGCTTTCTTGGGC3'
CF	5' CCTATATACCACCGTCGTC3'
CR	5' AGGATTATTGCTGCGGCGGTT3'
DF	5' CGAGCCTAGTTATAGCTGGT3'
DR	5' AGGGCTGTTATAGCAGCTAG3'
EF	5' CCTAGCCCATATGTCTTTGG3'
ER	5' AATACTAAATAGAGGGTGCC3'
FF	5' TCCTACGAAGTTAGCCTAGG3'
FR	5' AGGATTATTGCTGCGGCGGTT3'
GF	5' ATGAACCCCTACGTACTION3'
GR	5' ATACCAAAGCCTGGGAGGAT3'
HF	5' ACTTCATGAATAAATCCCC3'
HR	5' TCGATTGATGCTACCTCTCG3'
IF	5' ACAGCTAAGCGCTCTATCCA3'
IR	5' TGAAGGACGTCTTCAGCTGA3'
JF	5' CTGGCAGCAGGCATTACTAT3'
JR	5' GATTGGCTGTAAGTCGTACG3'
KF	5' ATAGGCGCTTTCGTACACTG3'
KR	5' CTGCAGTGCCTGATGTAAGT3'
LF	5' GTTGTCCCTGTAGAATCCCC3'
LR	5' TCCACATTTCGTAGGGGATA3'
MF	5' CGGGAATAGCGTTAGCCTTT3'
MR	5' ATAGGGGGTCAGTTGCTAAA3'
NF	5' TAATGGCACACCAAGCACAC3'
NR	5' GCGATTAGTGATTTCAGGTC3'
OF	5' ACTTCCAATCACCCGGTCTT3'
OR	5' TAGAAGCACGAGTGAACCAC3'
PF	5' CGCCTCCAAAGCTTAAACCT3'
PR	5' GGTATTTGCTTATTCAGCGGC3'
QF	5' CAAAAGCCCACGTAGAAGCT3'
QR	5' AATCGTTGGTCGGTTCTTAC3' ,

表二、用於台灣櫻花鉤吻鮭growth hormone gene 選殖的primer 序列

primer	sequence	Amplified region
F1	5' GTCAAGTCATCGAGTACGTTG3'	promoter, exon 1 , intron 1 and exon2(partial)
R1	5' TGACCGCGATGTTGAAGAGCC3'	
F2	5' GCTGATGCCAGTCTTACTGGT3'	exon 2, intron 2 and exon3
R2	5' TGAACTCTTCTGAGTCTCGTG3'	
F3	5' GACGGTACCCTGTTGCCTGAT3'	:exon 3. intron 3 and exon 4
R3	5' CGTGATGAGCAGATTGATGCC3'	
F4	5' AGATCTCTGAGAAGCTCAGCG3'	exon 4, intron 4 and exon 5
R4	5' TGTGCTAGTCCTTCTTGAAGC3'	
F5	5' CTACGAGTTGTTGGCTTGCTT3	exon 5, intron 5 and exon 6 to polyA additional signal
R5	5' GCAGAGAACAACAGATTTATT3'	

表三. 櫻鮭四亞種粒線體基因組結構

Gene	Position number								Size				Condon		Strain
	Amago		Biwa		Masu		Taiwan		A	B	M	T	start	stop	
	from	to	from	to	from	to	from	to							
D loop	1	998	1	998	1	998	1	998	998	998	998	998			H
tRNA^{phe}	999	1066	999	1066	999	1066	999	1066	68	68	68	68			H
12S rRNA	1067	2012	1067	2012	1067	2012	1067	2012	946	946	946	946			H
tRNA^{Val}	2013	2084	2013	2084	2013	2084	2013	2084	72	72	72	72			H
16S rRNA	2085	3763	2085	3763	2085	3763	2085	3763	1679	1679	1679	1679			H
tRNA^{Leu}	3764	3838	3764	3838	3764	3838	3764	3838	75	75	75	75			H
ND1	3839	4813	3839	4813	3839	4813	3839	4813	975	975	975	975	ATG	TAG	H
tRNA^{Ile}	4818	4889	4818	4889	4818	4889	4818	4889	72	72	72	72			H
tRNA^{Gln}	4887	4957	4887	4957	4887	4957	4887	4957	71	71	71	71			L
tRNA^{Met}	4957	5025	4957	5025	4957	5025	4957	5025	69	69	69	69			H
ND2	5026	6075	5026	6075	5026	6075	5026	6075	1050	1050	1050	1050	ATG	TAA	H
tRNA^{Trp}	6078	6147	6078	6147	6078	6147	6078	6147	70	70	70	70			H
tRNA^{Ala}	6149	6218	6149	6218	6149	6218	6149	6218	70	70	70	70			L
tRNA^{Asn}	6220	6292	6220	6292	6220	6292	6220	6292	73	73	73	73			L
OriL	6293	6325	6293	6325	6293	6325	6293	6325	33	33	33	33			L

tRNA^{Cys}	6326	6392	6326	6392	6326	6392	6326	6392	67	67	67	67			L
tRNA^{Tyr}	6393	6463	6393	6463	6393	6463	6393	6463	71	71	71	71			L
CO1	6465	8015	6465	8015	6465	8015	6465	8015	1551	1551	1551	1551	GTG	TAA	H
tRNA^{Ser}	8016	8086	8016	8086	8016	8086	8016	8086	71	71	71	71			L
tRNA^{Asp}	8090	8163	8090	8163	8090	8163	8090	8163	74	74	74	74			H
CO2	8178	8868	8178	8868	8178	8868	8178	8868	691	691	691	691	ATG	T—	H
tRNA^{Lys}	8869	8942	8869	8942	8869	8942	8869	8942	74	74	74	74			H
ATP8	8944	9111	8944	9111	8944	9111	8944	9111	168	168	168	168	ATG	TAA	H
ATP6	9102	9785	9102	9785	9102	9785	9102	9785	684	684	684	684	ATG	TAA	H
CO3	9785	10570	9785	10570	9785	10570	9785	10570	786	786	786	786	ATG	TAA	H
tRNA^{Gly}	10570	10639	10570	10639	10570	10639	10570	10639	70	70	70	70			H
ND3	10640	10988	10640	10988	10640	10988	10640	10988	349	349	349	349	ATG	T—	H
tRNA^{Arg}	10990	11058	10990	11058	10990	11058	10990	11058	69	69	69	69			H
ND4L	11059	11355	11059	11355	11059	11355	11059	11355	297	297	297	297	ATG	TAA	H
ND4	11349	12729	11349	12729	11349	12729	11349	12729	1381	1381	1381	1381	ATG	T—	H
tRNA^{His}	12730	12798	12730	12798	12730	12798	12730	12798	69	69	69	69			H
tRNA^{Ser}	12799	12867	12799	12867	12799	12867	12799	12867	69	69	69	69			H
tRNA^{Leu}	12869	12941	12869	12941	12869	12941	12869	12941	73	73	73	73			H
ND5	12942	14780	12942	14780	12942	14780	12942	14780	1839	1839	1839	1839	ATG	TAA	H
ND6	14777	15298	14777	15298	14777	15298	14777	15298	522	522	522	522	ATG	TAG	L
tRNA^{Glu}	15299	15367	15299	15367	15299	15367	15299	15367	69	69	69	69			L
Cytb	15371	16511	15371	16511	15371	16511	15371	16511	1141	1141	1141	1141	ATG	T—	H
tRNA^{Thr}	16512	16583	16512	16583	16512	16583	16512	16583	72	72	72	72			H
tRNA^{Pro}	16583	16652	16583	16652	16583	16652	16583	16652	70	70	70	70			L

表四、櫻鮭四亞種粒線體 protein coding genes 之胺基酸密碼使用表

Amino acid codon	Masu salmon	Amago salmon	Taiwan salmon	Biwas almon
Ala GCG	12	11	13	24
Ala GCA	95	99	105	210
Ala GCT	77	84	87	176
Ala GCC	120	132	140	280
Cys TGT	12	12	12	24
Cys TGC	16	16	16	32
Asp GAT	29	28	29	60
Asp GAC	35	45	45	90
Glu GAG	20	21	18	40
Glu GAA	86	85	88	172
Phe TTT	98	110	118	242
Phe TTC	100	109	110	216
Gly GGG	42	31	42	86
Gly GGA	78	95	97	194
Gly GGT	37	44	47	92
Gly GGC	60	56	61	120
His CAT	39	39	38	68
His CAC	60	69	71	148
Ile ATT	130	137	151	294
Ile ATC	113	116	123	250
Lys AAG	9	9	10	16
Lys AAA	66	67	64	134
Leu TTG	28	18	28	50
Leu TTA	106	106	116	236
Leu CTG	34	33	36	68
Leu CTA	172	160	192	386
Leu CTT	151	128	160	316
Leu CTC	113	112	123	252
Met ATG	39	38	38	80
Met ATA	104	107	117	226
Asn AAT	49	45	49	98
Asn AAC	56	64	66	132
Pro CCG	10	7	7	16

Pro CCA	60	72	74	144
Pro CCT	47	44	44	92
Pro CCC	85	71	86	170
Gln CAG	8	7	7	14
Gln CAA	92	86	93	186
Arg CGG	10	10	10	20
Arg CGA	44	40	45	88
Arg CGT	11	11	10	22
Arg CGC	9	7	9	20
Ser AGT	15	15	14	30
Ser AGC	39	36	39	76
Ser TCG	6	5	6	10
Ser TCA	55	58	55	110
Ser TCT	57	56	58	118
Ser TCC	72	69	71	144
Thr ACG	11	11	11	20
Thr ACA	97	97	106	214
Thr ACT	65	74	75	148
Thr ACC	115	109	116	226
Val GTG	27	15	26	48
Val GTA	76	84	87	184
Val GTT	61	70	71	140
Val GTC	41	40	39	86
Trp TGG	11	10	10	24
Trp TGA	100	111	111	218
Tyr TAT	40	48	49	102
Tyr TAC	61	59	62	120
End AGG	0	0	0	0
End AGA	0	1	0	0
End TAG	3	3	3	4
End TAA	7	6	7	14

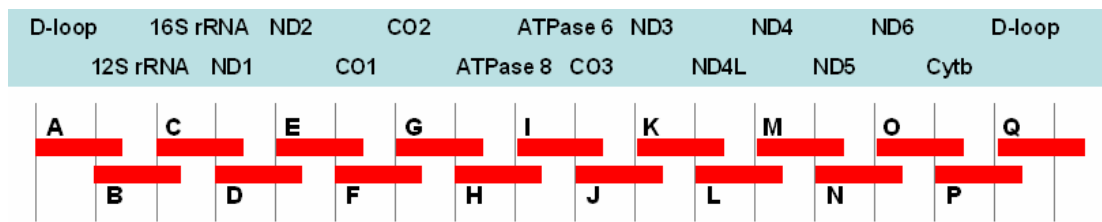
表五. 鮭科各物種間粒線體 DNA 鹼基對變異數目

Species	Taiwan salmon1	Taiwan salmon7	Amago salmon1	Amago salmon5	Masa salmona	Biwa salmona	Chiaook salmona	Chum salmona	Rainbow trout	Coho salmona	Cutthroat trout	Sockeye salmona	Char	Atlantic salmona	Brook trout	Comoa whitefish
Taiwan salmon1	0															
Taiwan salmon 7	10	0														
Amago salmon 1	61	61	0													
Amago salmon5	71	71	12	0												
Masa salmon	61	63	46	56	0											
Biwa salmon	142	144	128	138	133	0										
Chiaook salmon	1097	1099	1088	1099	1093	1092	0									
Chum salmon	1101	1101	1089	1100	1095	1090	138	0								
Rainbow trout	1103	1104	1092	1103	1099	1088	983	1004	0							
Coho salmon	1110	1110	1099	1108	1105	1108	690	724	990	0						
Cutthroat trout	1186	1186	1171	1182	1172	1176	1074	1080	768	1042	0					
Sockeye salmon	1195	1195	1175	1186	1186	1188	1118	1124	1073	1104	1128	0				
Char	1659	1660	1649	1660	1651	1664	1624	1629	1602	1603	1650	1729	0			
Atlantic salmon	1677	1678	1664	1675	1671	1679	1624	1639	1586	1610	1633	1699	1560	0		
Brook trout	1746	1746	1740	1751	1743	1749	1687	1699	1650	1680	1713	1805	749	1640	0	
Common Whitefish	2263	2263	2263	2273	2254	2250	2236	2227	2235	2199	2236	2291	2240	2129	2274	0

表六. 鮭科各物種完整粒線體 DNA 序列以 Kimura-2-parameter 法計算出之遺傳距離(genetic distance)

Species	Taiwan salmon1	Taiwan salmon7	Amago salmon1	Amago salmon5	Masu salmon	Biwa salmon	Chinook salmon	Chum salmon	Rainbow trout	Coko salmon	Cutthroat trout	Snakeeye salmon	Char	Atlantic salmon	Brook trout	Common whitefish
Taiwan salmon1	0															
Taiwan salmon 7	0.0006	0														
Amago salmon 1	0.0037	0.0037	0													
Amago salmon5	0.0043	0.0043	0.0007	0												
Masu salmon	0.0037	0.0038	0.0028	0.0034	0											
Biwa salmon	0.0087	0.0088	0.0078	0.0084	0.0081	0										
Chinook salmon	0.0703	0.0704	0.0697	0.0704	0.07	0.0699	0									
Chum salmon	0.0705	0.0705	0.0697	0.0705	0.0701	0.0698	0.0084	0								
Rainbow trout	0.0708	0.0708	0.07	0.0708	0.0705	0.0698	0.0626	0.064	0							
Coko salmon	0.0712	0.0712	0.0705	0.0711	0.0709	0.0711	0.0433	0.0455	0.0631	0						
Cutthroat trout	0.0765	0.0765	0.0755	0.0762	0.0755	0.0759	0.0688	0.0691	0.0485	0.0667	0					
Snakeeye salmon	0.0771	0.0771	0.0757	0.0764	0.0764	0.0766	0.0717	0.0721	0.0687	0.0708	0.0725	0				
Char	0.1094	0.1095	0.1087	0.1095	0.1088	0.1098	0.1069	0.1072	0.1053	0.1054	0.1089	0.1145	0			
Atlantic salmon	0.1108	0.1109	0.1098	0.1106	0.1104	0.111	0.1069	0.108	0.1043	0.106	0.1078	0.1124	0.1025	0		
Brook trout	0.1156	0.1156	0.1152	0.116	0.1154	0.1158	0.1113	0.1121	0.1086	0.1108	0.1133	0.12	0.0471	0.1081	0	
Common Whitefish	0.1537	0.1537	0.1537	0.1545	0.153	0.1527	0.1518	0.1511	0.1517	0.1489	0.1519	0.156	0.1522	0.1439	0.1548	0

圖一、台灣鮭魚粒線體 DNA 定序中各 PCR 反應的放大部位。

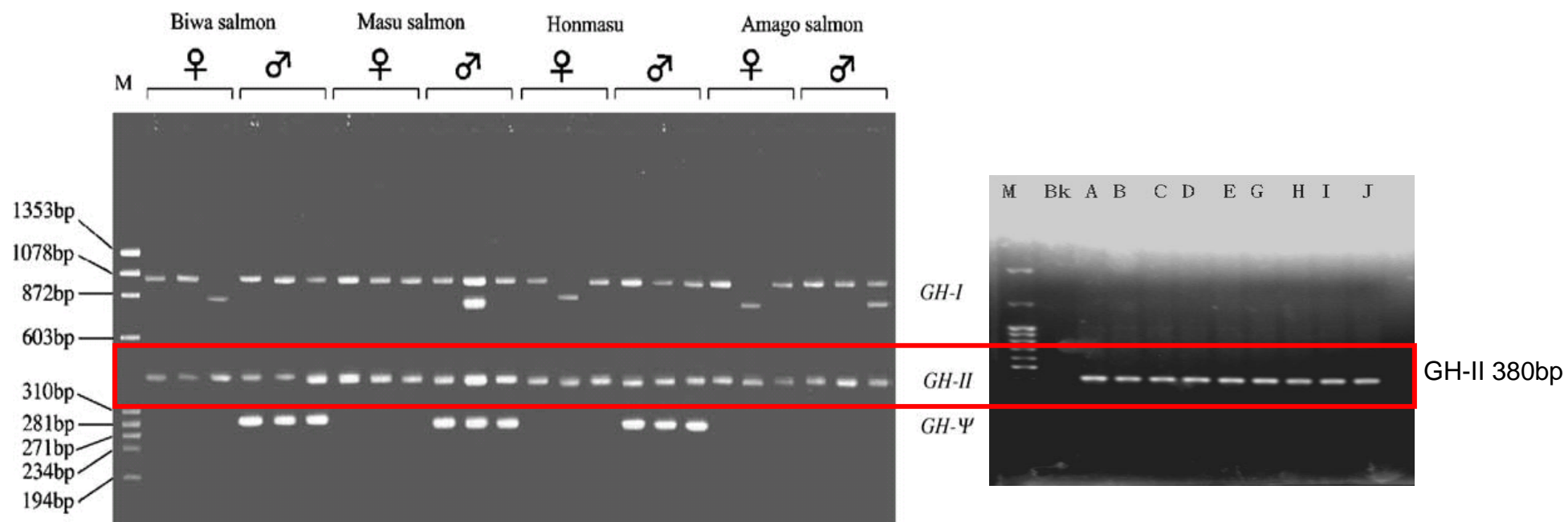


	(34)	34	40	50	60	70	80	90	103
rainbow trout GH1 intron3	(34)	ATGCCCTTIAGAACCAIATAAAAGTGTCAAATCG	-----	C	-----	TATTCACCTTAAATATGAACTCC			
Taiwan salmon A GH1 intron 3	(34)	ATGCCCTTIAGAACCAIATAAAAGTGTCA	ATCG	TCACAGTTTC	CACTC	TATTCACCTTAAATATGAACTCC			
Taiwan salmon B GH1 intron 3	(34)	ATGCCCTTIAGAACCAIATAAAAGTGTCA	ATCG	TCACAGTTTC	CACTC	TATTCACCTTAAATATGAACTCC			
Taiwan salmon CGH1 intron 3	(34)	ATGCCCTTIAGAACCAIATAAAAGTGTCA	ATCG	TCACAGTTTC	CACTC	TATTCACCTTAAATATGAACTCC			
	(440)	440	450	460	470	480	490	509	
rainbow trout GH1 intron3	(426)	GGGCGGCACACAATTCTCCAGC	GTCGTTAGGGTTTGCCGGGTTGCAATACCTC	AGTGTCTTCAACTAA					
Taiwan salmon A GH1 intron 3	(435)	GGGCGGCACACAATTCTCCAGC	-----	-----	-----	-----	-----	AGTGTCTTCAACTAA	
Taiwan salmon B GH1 intron 3	(435)	GGGCGGCACACAATTCTCCAGC	-----	-----	-----	-----	-----	AGTGTCTTCAACTAA	
Taiwan salmon CGH1 intron 3	(435)	GGGCGGCACACAATTCTCCAGC	-----	-----	-----	-----	-----	AGTGTCTTCAACTAA	
	(567)	567	580	590	600	610	620	636	
rainbow trout GH1 intron3	(553)	TCGGTGGTTTCTCTAC	GTCTACAT	CTCCGTT	TTGTGCTTTTCTGTACAGGAA	CCCGCCCCAAAAGTAT			
Taiwan salmon A GH1 intron 3	(529)	TTGGTGGTTTCTCTAC	ATCTCCATT	-----	TTGTGCTTTTCTGTACAGGAA	CCCGCCCCAAAAGTAT			
Taiwan salmon B GH1 intron 3	(529)	TTGGTGGTTTCTCTAC	ATCTCCATT	-----	TTGTGCTTTTCTGTACAGGAA	CCCGCCCCAAAAGTAT			
Taiwan salmon CGH1 intron 3	(529)	TTGGTGGTTTCTCTAC	ATCTCCATT	-----	TTGTGCTTTTCTGTACAGGAA	CCCGCCCCAAAAGTAT			

圖二、比對台灣鮭魚與虹鱒的GH I之 intron 3 序列，發現兩物種有極大的差異。

	(51)	51	60	70	80	90	100	110	121
arrago GH1 intron 3	(51)	ATAAAGTGTGAGATCGTGACAGTTTC	CACTCTGC	TATTCACCTTAAATATGA	AACTCCTCCATGATGCAAGAT				
masu GH1 intron3	(51)	ATAAAGTGTGAGATCGTGACAGTTTC	CACTCTGC	TATTCACCTTAAATATGA	AACTCCTCCATGATGCAAGAT				
Taiwan salmon GH1 intron 3	(51)	ATAAAGTGTGAGATCGTGACAGTTTC	-----	-----	TATTCACCTTAAATATGA	AACTCCTCCATGATGCAAGAT			

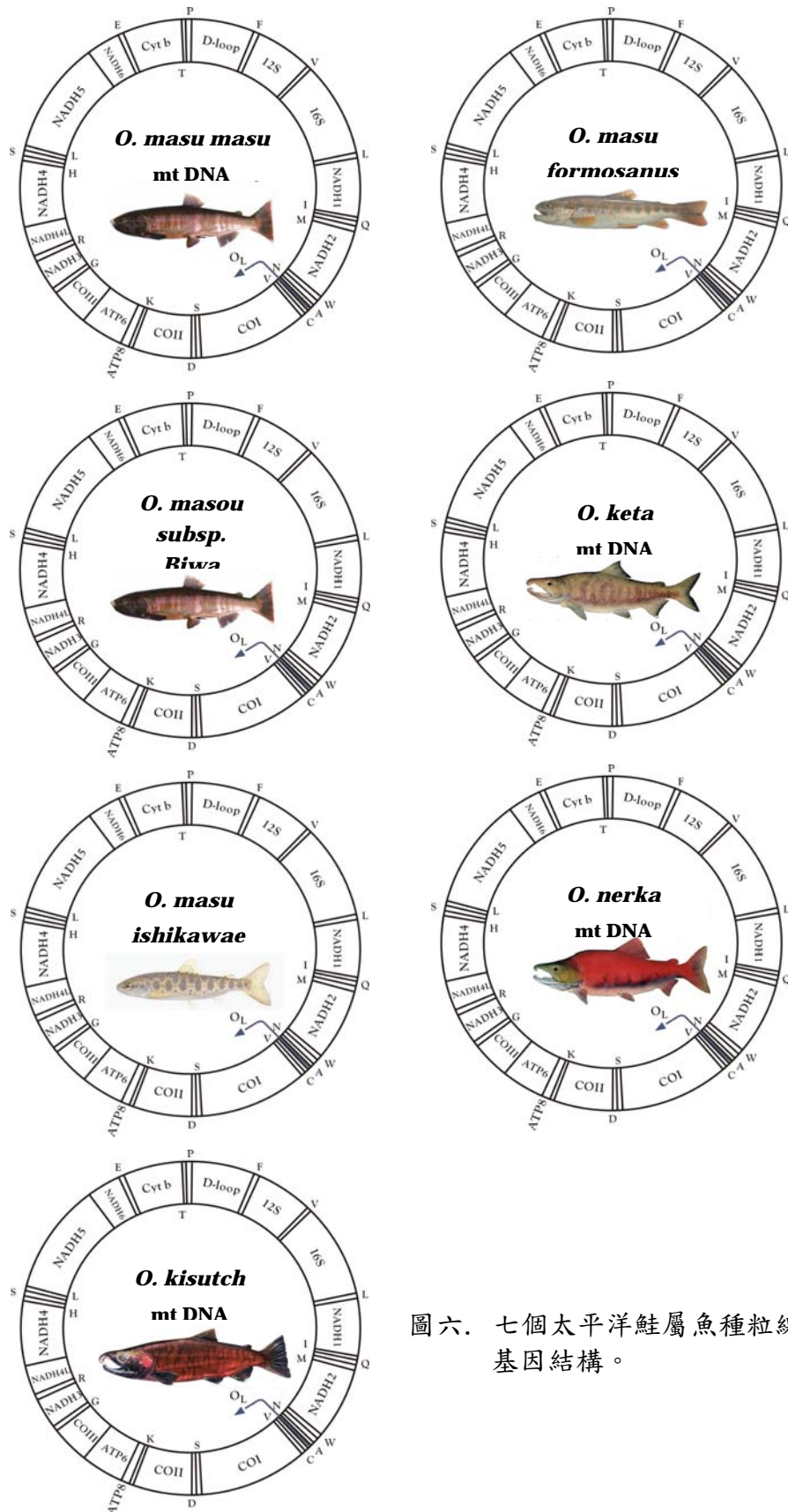
圖三、在GH I之 intron 3的部分發現台灣鮭魚有一段TCG三個核酸鹼基對的缺失，而其他櫻鮭家族亞種（櫻鮭與石川鮭魚）此段的基因均無此現象。



圖四、台灣鮭魚的基因體中沒有生長荷爾蒙的pseudogene GH- ϕ 存在

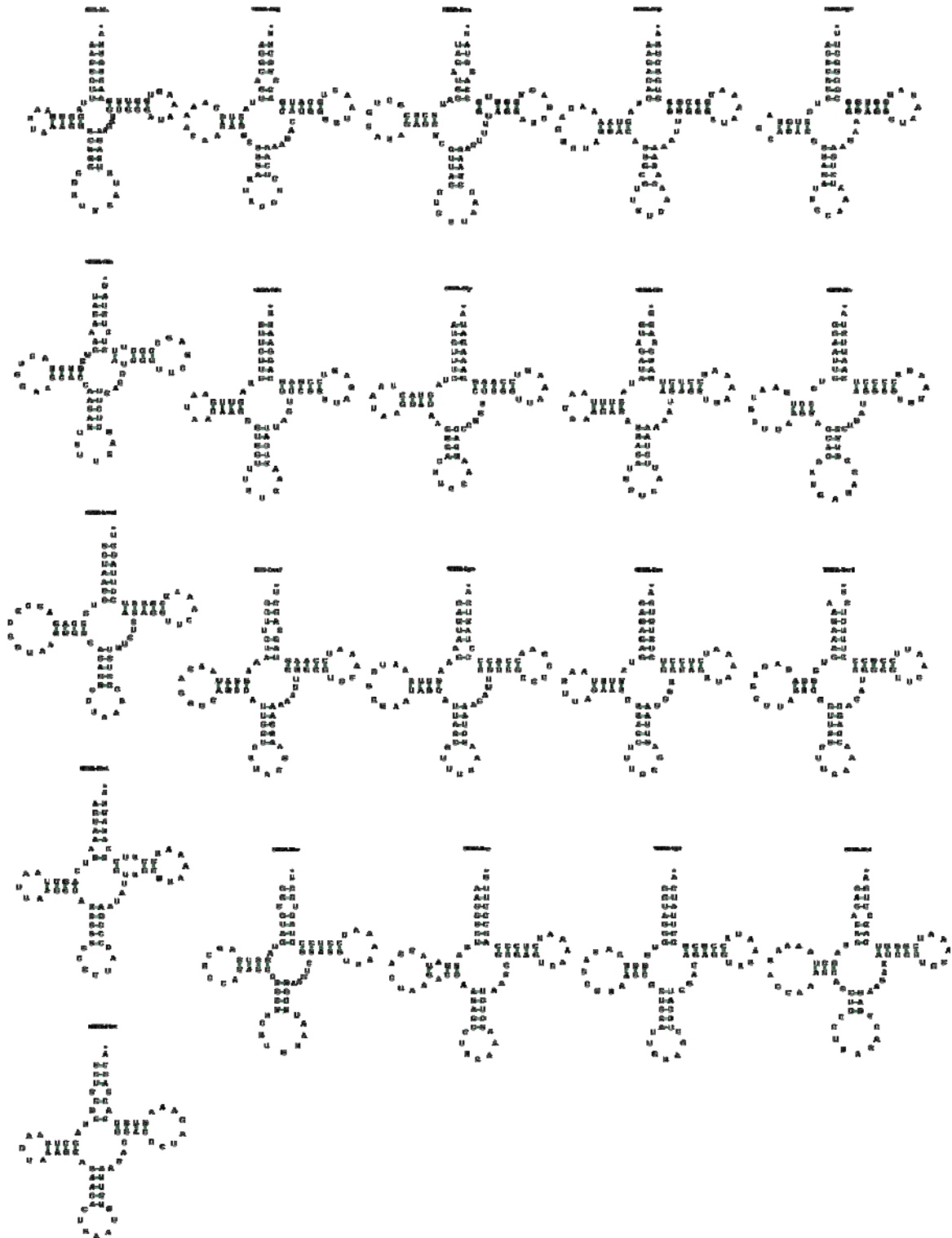
	(266) 266	280	290	300	318
A (264)	ACTATAACCTATTCTTCTTGTCCCCCCCCCAAAGGTTGAGACCTACCTGACC				
E (265)	ACTATAACCTATTCTTCTTGTCCCCCCCCCAAAGGTTGAGACCTACCTGACC				
G (265)	ACTATAACCTATTCTTCTTGTCCCCCCCCCAAAGGTTGAGACCTACCTGACC				
B (265)	ACTATAACCTATTCTTCTTGTCCCCCCCCCAAAGGTTGAGACCTACCTGACC				
D (265)	ACTATAACCTATTCTTCTTGTCCCCCCCCCAAAGGTTGAAACCTACCTGACC				
I (265)	ACTATAACCTATTCTTCTTGTCCCCCCCCCAAAGGTTGAAACCTACCTGACC				
C (265)	ACTATAACCTATTCTTCTTGTCCCCCCCCCAAAGGTTGAGACCTACCTGACC				
H (266)	ACTATAACCTATTCTTCTTGTCCCCCCCCCAAAGGTTGAGACCTACCTGACC				
J (265)	ACTATAACCTATTCTTCTTGTCCCCCCCCCAAAGGTTGAGACCTACCTGACC				
Consensus (266)	ACTATAACCTATTCTTCTTGTCCCCCCCCCAAAGGTTGAGACCTACCTGACC				

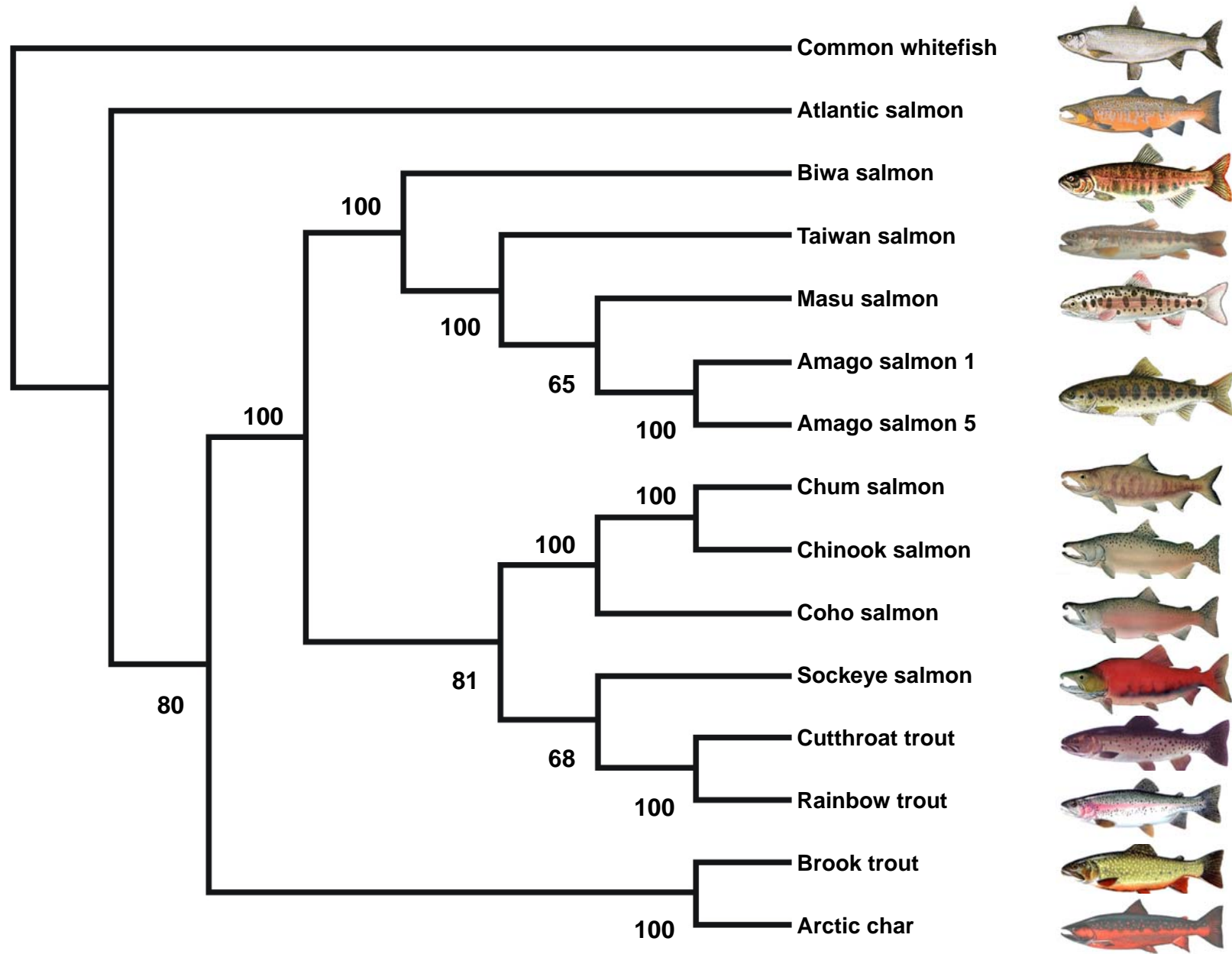
圖五. 九個台灣鮭魚檢體的 GH2 基因 exon 6 部位僅有有一個A/G的 heterozygotes。



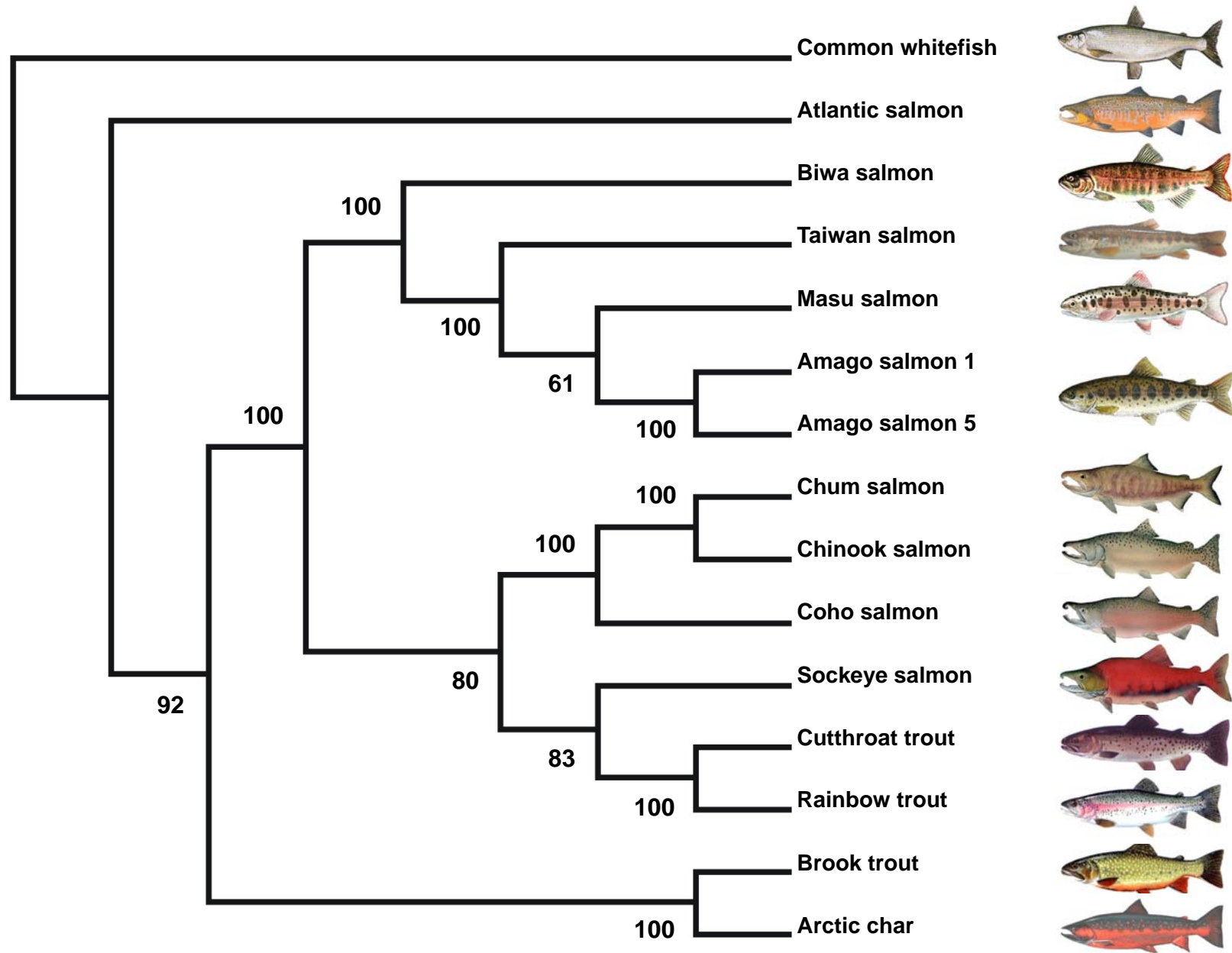
圖六. 七個太平洋鮭屬魚種粒線體基因結構。

圖七、用於台灣櫻花鉤吻鮭growth hormone gene 選殖的primer 序列

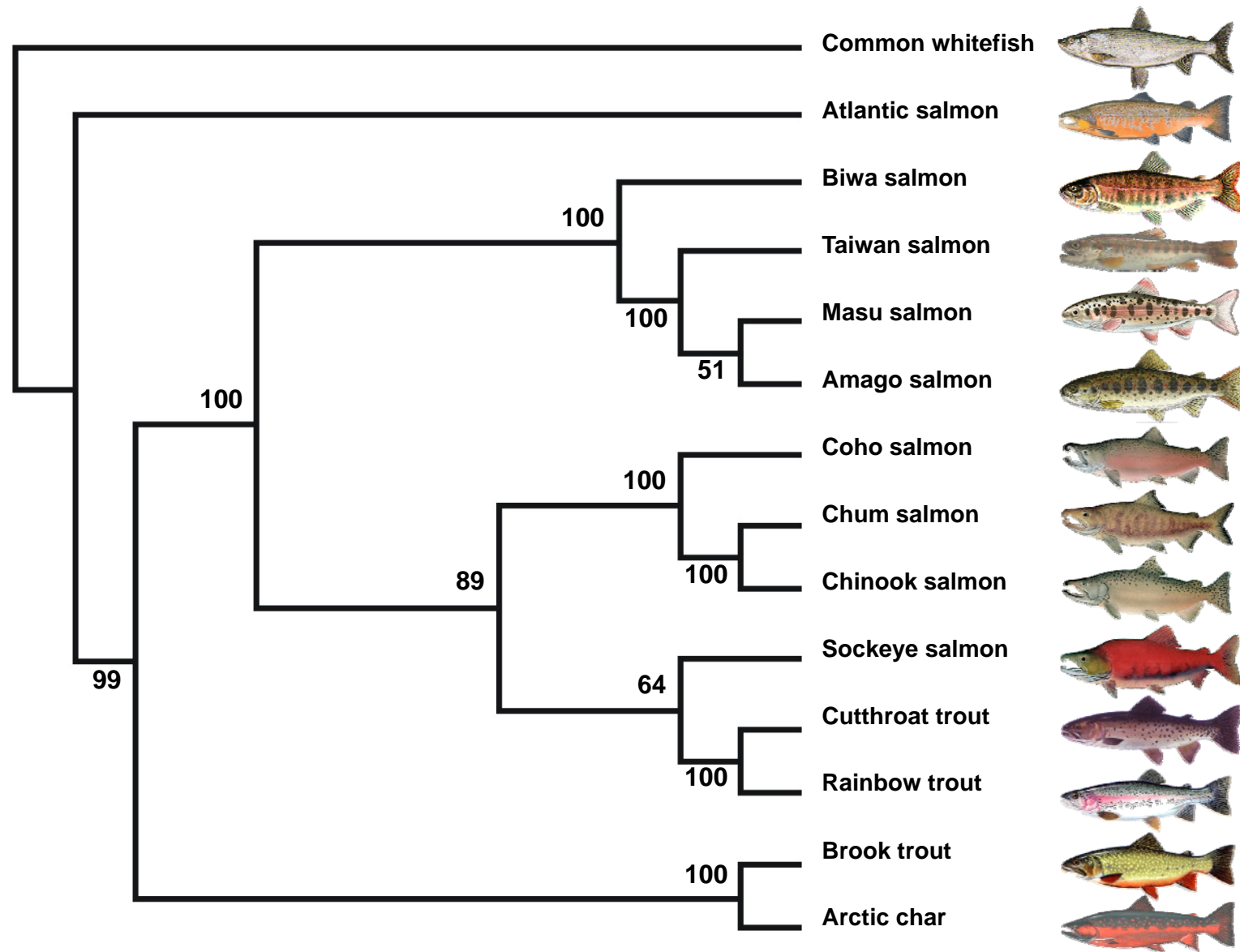




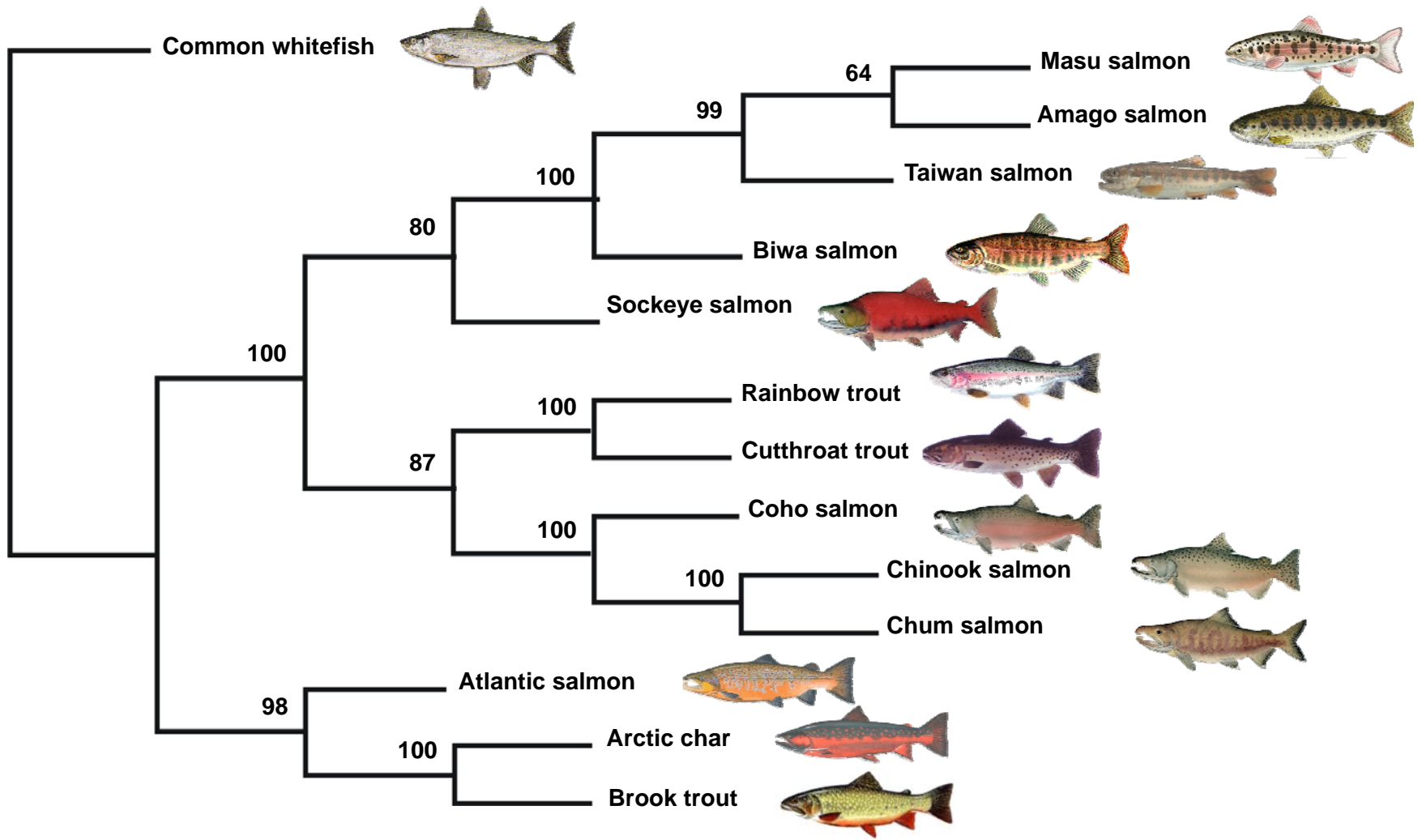
圖八、利用完整的粒線體的序列以 Common whitefish 做為外群，使用鄰接法(Neighbor-Joining ; NJ)建構的演化樹



圖九、利用完整的粒線體的序列以 Common whitefish 做為外群，使用最小進化法(Minimum Evolution; ME)建構的演化樹



圖十、利用完整的粒線體的序列以 Common whitefish 做為外群，使用最大簡約法(Maximum Parsimony ; MP)建構的演化樹

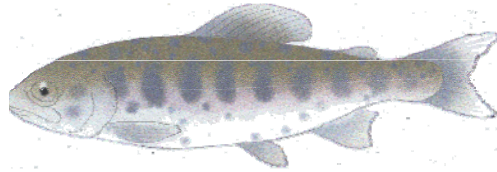


圖十一、利用完整的粒線體的序列以 Common whitefish 做為外群，使用最大似然法(Maximum Likelihood; ML)建構的演化樹

圖十二、櫻鮭四大亞種形態與解剖學上的異同

亞種	體側紅點	側線鱗片數	體側鱗片數	背鰭軟條數	胸鰭軟條數	臀鰭軟條數	脊椎骨數
Taiwan salmon	無	130-146	136-150	12-15(13)	12-14(13)	11-14(13)	60-63(62)
Yamame	無	130-139	132-148	14-17(15)	12-16(14)	14-16(15)	63-66(64)
Amago	仔魚，成魚均有	126-138	132-148	14-17(15)	13-17(15)	13-16(15)	63-66(64)
Biwa salmon	仔魚有，成魚無	128-138	114-147	14-17(15)	14-16(15)	14-15(14)	63-66(64)

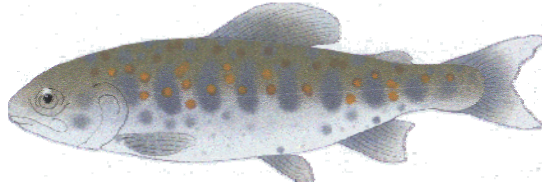
Taiwan salmon



Yamame



Amago



Biwa salmon

