台灣東北部卯澳灣海域之海膽生物多樣性研究

Biodiversity of Sea Urchins in the Maoaw Bay of the Northeastern Taiwan

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摘 要

本研究以二階段方式調查台灣東北部卯澳灣海域的海膽種類及數量。首先依據該海灣底質特性劃分爲第Ⅰ、Ⅱ、Ⅲ、Ⅳ及Ⅴ區五個小海區。第一階段，在第Ⅰ、Ⅱ、Ⅳ區三個小海區中分別隨機選取1個點，第Ⅴ區隨機選取2個點，以長100m，寬1m的穿越線，進行垂直海岸的抽樣調查；第二階段再依據第一階段的結果，分別選取水深3m、6m、9m三種深度，進行等深線的詳細抽樣調查。調查過程中，記錄海膽的種類、數量及深度，並輔以拍照。

在第一階段垂直海岸的抽樣調查中，所有海膽種類密度隨著深度的不同呈現顯著差異。在第二階段27條等深線的調查中，共記錄了5科11種2,901隻海膽，其中以白尖紫叢海膽(*Echinostrephus aciculatus*)的密度最高，其密度爲88.81隻/100m^2，梅氏長海膽(*Echinometra mathaei*)次之，其密度爲16.33隻/100m^2，其餘種類密度均低於10隻/100m^2，依序分別爲紫海膽(*Anthocidaris crassispina*)、紫叢海膽(*Echinostrephus molaris*)、口鰓海膽(*Stomopneustes variolaris*)、環鋸棘頭帕海膽(*Pionocidaris baculosa*)、刺冠海膽(*Diadema setosum*)、冠棘眞頭帕海膽(*Ecuidaris metularia*)、白棘三列海膽(*Tripeustes gratilla*)、環刺棘海膽(*Echinothrix calamaris*)及藍環冠海膽(*Diadema sevignyi*)。在整個海域中，白尖紫叢海膽的密度與其他10種海膽的密度有顯著差異，其數量在第Ⅰ、Ⅱ、Ⅳ區，大多數集中在3m的深度，6m次之，9m非常少，而在第Ⅴ區則大多集中在9m的深度。歧異度指數值無論在小海區或深度均低，而整個海域歧異度指數值隨著優勢種白尖紫叢海膽密度增加呈現遞減趨勢，顯示本海域海膽種類隨著海區、深度及底質不同，呈現多樣性分布。

Abstract

The community structure and abundance of sea urchins in the Maoaw Bay of the northeastern Taiwan was surveyed in July to September 2002. A total of 2,901 individuals in 11 species of five families were collected. *Echinostrephus aciculatus* was the most dominant species and had an average density of 88.81 individuals/100m^2, while *Echinometra mathaei* was the secondly abundant at 16.33 individuals/100m^2. They were followed by the remaining nine species in a decreasing order from *Anthocidaris crassispina* to *Echinostrephus molaris*, *Stomopneustes variolaris*, *Pionocidaris baculosa*, *Diadema setosum*, *Ecuidaris metularia*, *Tripeustes gratilla*, *Echinothrix calamaris*, and then to *Diadema sevignyi*. Average densities of these species were less than 10 individuals/100m^2. There were low values in species richness indices (ranged between 1.51 and 2.84), Simpson's species diversity indices (0.12 and 0.36), Shannon's species diversity indices (0.12 and 0.28), and Pielou's evenness indices (0.17 and 0.37). The low values were primarily due to the low number of the species and a skew distribution of their abundance, resulted from the high dominancy of a single species *E. aciculatus*. Each of the indices showed a decreasing trend with the increase in the abundance of *E. aciculatus*. The abundance of sea urchins differed by species, depths and sampling areas, suggesting that local environmental and oceanographic conditions determine the sea urchin community structure and abundance in the Maoaw Bay of Taiwan.

關鍵詞：海膽、群聚結構、生物多樣性、台灣東北部

Key words : sea urchin, community structure, biodiversity, northeastern Taiwan

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緒　言

台灣東北部海域泛指東經121°65’至122°15’，北緯24°50’至25°25’之間。範圍北起台北縣瑞芳鎮南雅里，南至宜蘭縣頭城鎮之狹長海岸線，全長約66 km。海域範圍由鼻頭角至三貂角一線，約計4,275 ha。在這一片山海交錯、峽灣凹凸的崎嶇海岸線中，擁有海灣、斷崖、溪流、海蝕平台、礫石灘、沙灘、珊瑚礁等豐富地形和不同的生態環境，尤其本區位處黑潮暖流與大陸沿岸冷流的交會地區，不同的海流與充足的營養鹽造就了豐富又多樣的海洋生物資源(黃 2000)。

台灣東北部海域靠近三貂角田寮鼻一側有一個狹小的卯澳灣，該海灣擁有相當豐富的海洋生物資源，例如九孔、龍蝦、海膽、

石花菜等等，於1976年起已被公告畫設爲漁業資源保育區。以往曾經有許多調查與研究在此海灣進行，包括有魚類相(邵 1989；何 1994)、仔稚魚苗相(曾 1985)、海藻種類(王 1978；黃 1999)、珊瑚種類(楊及戴 1982)、九孔資源(曾 1994，1996；林 2001；辜 2002；Lee *et al.* 2002)，與全面性的自然資源與環境調查(曾 1990，1991；張等 1992；鄭等 1994，1996，1997，1998)。其中有關該海域的海膽研究也曾被調查與研究(陳及張 1981；白 1982；游等 1992；鄭等 1994，1996，1997，1998；Chao 2000)。

海膽在分類上是屬於棘皮動物門(ECHINODERMATA)、海膽綱(ECHINOIDEA)，全世界約有900種，分屬於13個目，其個體呈半球型或平扁型，可區分爲體輻對稱之對稱亞綱(Regularia)的正型海膽，及不對稱之歪型亞綱(Irregularia)的歪型海膽(Pechenik 2000)。在關於台灣海膽的研究中，日籍學者早阪一郎曾發表了13種台灣產的正型海膽報告(Hayasaka 1948)，爲第一篇關於海膽的分類研究；陳及張(1981)曾進行台灣正型海膽的種類調查，共記錄了21種，其中8種爲新紀錄種；Chao (2000)也發表了台灣有19種歪型海膽，其中6種爲新紀錄種。除了上述分類學的調查研究外，有關海膽生殖生物學的相關研究也有多篇報告(葛 1980；林 1995；Chen 1989；Chen and Chen 1993；Chen and Chen 1995)。

海膽爲底棲性生物，在底棲生態系上扮演著很重要的角色(Sammarco 1980；McClanahan 1997)。由於海膽多半爲藻食性或以有機碎屑爲食，藉由高度特化之口部構造(Aristole's lantern)在礁岩表面刮食，會間接地影響許多藻食性魚類及其他底棲性無脊椎動物的豐富度(Fletcher 1987；Holbrook *et al.* 1990；Jones and Andrew 1990)。海膽亦會造成生物侵蝕(bioerosion)，其攝食的過程中除了會刮食藻類外，也同時移除底質上的碳酸鹽類，對珊瑚礁的成長及珊瑚礁生態系中有機碳與無機碳的轉換(turnover)造成影響。至於人類對海膽之掠食者的漁撈行爲則會間接地造成其族群數量的增加，最終可能導致整個底棲生態系的崩解(Silva and McClanahan 2001)。

在卯澳灣中，過去曾盛產數量衆多且優質的海膽資源，近年來在人類大量採捕與海域棲息環境變動下，可能也會造成資源量衰減與群聚結構的改變。然而海膽具有不任意變換巢穴的習性(Mortensen 1943；Grunbaum *et al.* 1978；Russo 1980；Carpenter 1981)，其種類與數量可相當程度反應環境的變化。另一方面，過去台灣東北部海域有關海膽群聚分布的研究多是研究計畫中的一部分，且多爲定性的種類描述，少有定量的調查與分析。因此本研究針對卯澳灣海域的海膽種類、族群數量與分布進行調查，並探討海膽種類的歧異度，以期對該海域的海膽群聚結構有更進一步的了解。

材料與方法

卯澳灣爲一個三角形海灣，灣口朝向北北東方，灣內左深右淺，底質環境並非均質(圖1)，過去針對該海域九孔資源的調查研究，將該海灣劃分爲五個小海區，其中第Ⅰ區爲整個海灣水深較淺的區域，近岸附近有沙石分布，其餘底質以礁岩爲主，第II區的底質除礁岩外，並有些許沙地交錯其中，靠灣口處則有一些大型鵝卵石，第III區位在灣口，水深較深，兩側爲礁岩，中間也有些許沙地分布其間，第IV區的地勢落差大，近岸處有許多大型的鵝卵石，離岸較遠處爲平坦的礁岩，及第Ⅴ區是卯澳灣左側之外的一個小海灣，其底質多爲開闊的礁岩平台(Lee *et al.* 2002)。

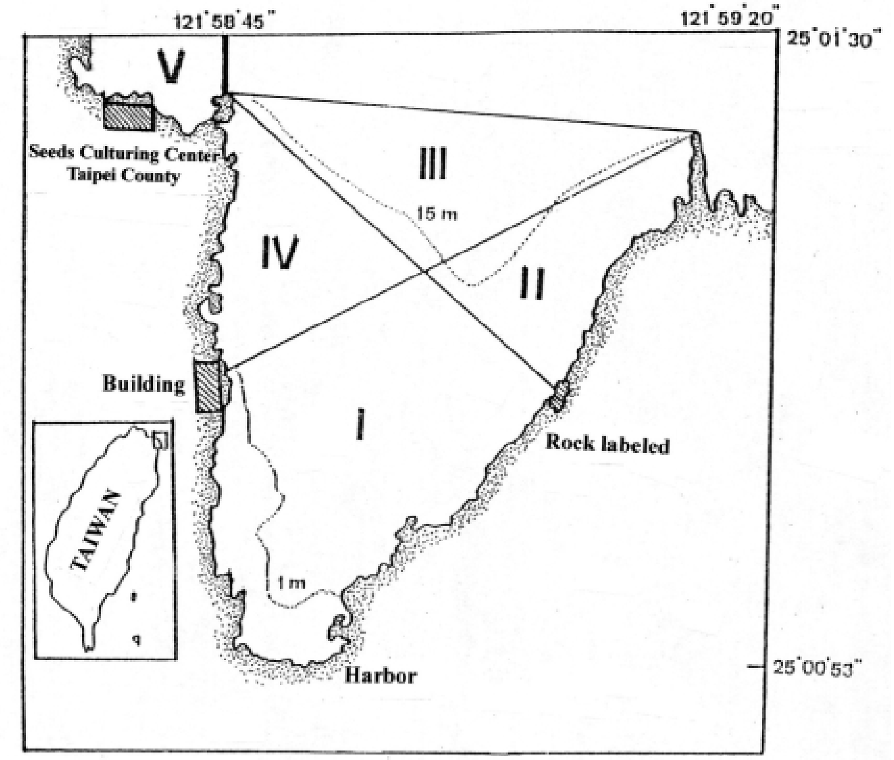


圖 1.台灣東北部卯澳灣調查海域 (引述自Lee *et al.* 2002)。

Fig. 1. The study area: the Maoaw Bay in the northeastern Taiwan (After Lee *et al*. 2002).

本研究亦按照上述五個小海區的劃分方式，分別調查海膽的種類與數量。自2002年7月至9月，分兩個階段進行調查。第一階段，在第Ⅰ、Ⅱ、Ⅳ區三個小海區中分別隨機選取1個點，第Ⅴ區隨機選取2個點，以長100m，寬1m垂直海岸的穿越線(transect line)，調查各小海區的海膽種類、數量與深度，並輔以拍照記錄。接著，根據第一階段的結果，選擇三種深度，以進行第二階段分區、分深度的詳細調查。第二階段的調查，由一位熟悉卯澳灣海域的漁民陪同研究人員，分別沿著三種深度的等深線進行調查，其中3m等深線有14條，6m等深線有8條，9m等深線有5條，合計有27條100m^{2}抽樣調查線；若依據小海區統計，則第Ⅰ區有9條，第Ⅱ區有8條，第Ⅳ區有8條，第Ⅴ區有2條抽樣調查線。每次調查皆以水肺潛水與船潛的方式在當天的09 : 00 至14 : 00之間進行。

海膽歧異度的估算係採用生態學中常用的四個指數：種豐度指數(Species richness index)、歧異度指數(Simpson's index)、歧異度指數(Shannon's index)，及均勻度指數(Pielou's evenness index)進行。四個指數之定義如下：

Species richness index:

$d = (S\text{-}1)/\log N$，S爲種數，N爲總隻數 (Margalef 1958)；

Simpson's index:

$c = 1 - \sum_{i=1}^{s} (n_i / N)^2$，其中$n_i$爲第i種隻數，$N$爲總隻數 (Simpson 1949)；

Shannon's index:

$H = -\sum_{i=1}^{s} (n_i / N)*\log(n_i / N)$，其中$n_i$爲第i種隻數，$N$爲總隻數 (Shannon and Weaver 1949)；

Pielou's evenness index:

$e = H / \log S$，其中H爲Shannon's index，S爲種數 (Pielou 1966)。

並利用Kruskal-Wallis test (Sokal and Rohlf 1995) 無母數統計分析法檢定各小海區間、各深度間，以及各種類間的密度差異。

結 果

第一階段在第Ⅰ、II、Ⅳ區各一條穿越線，及第Ⅴ區二條穿越線調查中，共記錄了850隻海膽，其中大多數爲白尖紫叢海膽(*Echinostrephus aciculatus*)與梅氏長海膽(*Echinometra mathaei*)。所有海膽種類的密度隨著深度的不同呈現顯著差異(p=0.03<0.1) (圖2)，其中水深0-4.5m，平均3m的密度爲79.80隻/100m^2；水深4.5-7.5m，平均6m的密度爲87.20隻/100m^2；水深7.5m以下，平均9m的密度爲0.60隻/100m^2，其中水深3m與6m的密度間(p=0.40>0.1)及6m與9m的密度間(p=0.13>0.1)無顯著差異，但是水深3m與9m的密度間有顯著差異 (p=0.01<0.1) (表1)。

依據第一階段調查的結果，顯示平均水深3m、6m、9m深度的海膽呈現不同密度值，因此本研究再選取3m、6m、9m三個深度作爲第二階段依據等深線的抽樣調查。

在第二階段27條抽樣調查線中，共記錄了5科11種2,901隻海膽，其中以長海膽科的白尖紫叢海膽數量最多，其密度爲88.81隻/100m^2，梅氏長海膽密度16.33隻/100m^{2}次之，其餘9種海膽的密度均低於10隻/100m^2，其密度依序爲，紫海膽(*Anthocidaris crassispina*) 1.11隻/100m^2，紫叢海膽(*Echinostrephus molaris*) 0.30隻/100m^2，口鰓海膽(*Stomopneustes variolaris*) 0.26隻/100m^2，環鋸棘頭帕海膽(*Pionocidaris baculosa*) 0.19隻

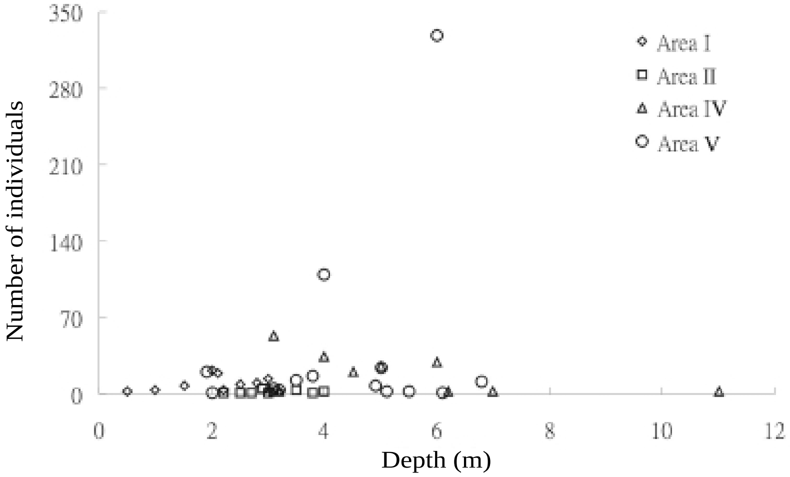


圖2. 台灣東北部卯澳灣海域第一階段垂直海岸穿越線調查各種深度之海膽數量。

Fig. 2. The relationship between the number of sea urchin and depth at the four sampling areas of the Maoaw Bay in the northeastern Taiwan obtained in the preliminary survey.

/100m^2，刺冠海膽(*Diadema setosum*) 0.15隻/100m^2，冠棘眞頭帕海膽(*Ecuidaris metularia*) 0.11隻/100m^2，白棘三列海膽(*Tripeustes gratilla*) 0.11隻 /100m^2，環刺棘海膽(*Echinothrix calamaris*) 0.04隻/100m^2，及藍環冠海膽(*Diadema sevignyi*) 0.04隻/100m^2。在整個卯澳灣海域中，白尖紫叢海膽的密度與其他10種海膽的密度間有顯著差異($p<0.1$) (表2)。在第Ⅰ、Ⅱ、Ⅳ區，海膽大多數分布在3m的深度，6m次之，9m除在第Ⅳ區有少數外幾乎無海膽分布；然而在第Ⅴ區，則是完全相反，海膽幾乎集中在9m深度。若就整個

表 1. 台灣東北部卯澳灣海域第一階段垂直海岸穿越線調查各種深度之海膽密度

Table 1. Densities (mean ± standard deviations; maximum and minimum in parenthese) of sea urchins obtained from the preliminary phase of the survey at different depths along the vertical transects in the Maoaw Bay of the northeastern Taiwan

Depths (m)	Number of samples	Density (ind./100m^2)
3	5	79.80 ± 50.93 (134 - 18)^{a}
6	5	87.20 ± 144.61 (342 - 0)^{ab}
9	5	0.60 ± 1.34 (6 - 0)^{b}

a,b : Mean densities followed by the same superscripts, a or b, are not significant difference (Kruskal-Wallis test, p>0.05).

表 2. 台灣東北部卯澳灣海域各種海膽全海區密度

Table 2. Densities (mean ± standard deviations; maximum and minimum in parentheses; ind./100m^2) of sea urchins by species in the Maoaw Bay of the northeastern Taiwan

Species	Chinese name	Replications	Density
Echinostrephus aciculatus	白尖紫叢海膽	27	88.81 ± 142.69 (465 - 0)^{a}
Echinometra mathaei	梅氏長海膽	27	16.33 ± 31.02 (153 - 0)^{b}
Anthocidaris crassispina	紫海膽	27	1.11 ± 1.63 (6 - 0)^{b}
Echinostrephus molaris	紫叢海膽	27	0.30 ± 0.87 (4 - 0)^{b}
Stomopneustes variolaris	口鰓海膽	27	0.26 ± 0.53 (2 - 0)^{b}
Prionocidaris baculosa	環鋸棘頭帕海膽	27	0.19 ± 0.56 (2 - 0)^{b}
Diadema setosum	刺冠海膽	27	0.15 ± 0.36 (1 - 0)^{b}
Ecuidaris metularia	冠棘眞頭帕海膽	27	0.11 ± 0.42 (2 - 0)^{b}
Tripeustes gratilla	白棘三列海膽	27	0.11 ± 0.42 (1 - 0)^{b}
Echinothrix calamaris	環刺棘海膽	27	0.04 ± 0.19 (1 - 0)^{b}
Diadema sevignyi	藍環冠海膽	27	0.04 ± 0.19 (1 - 0)^{b}

a,b : Mean densities followed by the same superscripts, a or b, are not significantly difference (Kruskal-Wallis test, p>0.05).

海域來說，海膽的分布以3m最多，9m次之，6m最少(圖3)。其中數量最多的優勢種白尖紫叢海膽的分布亦與全海區所有海膽的分布呈現相似的趨勢，即在第 I 、II 、IV區，大多數集中在3m的深度，而在第V區則集中在9m的深度(圖4)。

在四個小海區種類間的密度比較中，密度最高的白尖紫叢海膽在小海區間的密度並無顯著差異(p＝0.13>0.1)。密度次高者爲梅氏長海膽，其在第 I 區與第IV區(p＝0.09<0.1)，及第II區與第IV區(p＝0.09<0.1)之間的密度有顯著差異。其餘種類的密度均低，且在小海區之間均無顯著差異(p>0.1) (圖5)。

在三種深度種類間的密度比較中，亦皆以白尖紫叢海膽的密度最高，梅氏長海膽次之，其餘種類的密度均低，且在三種深度間均無顯著差異(p>0.1) (圖6)。

歧異度指數方面，四個小海區的Species

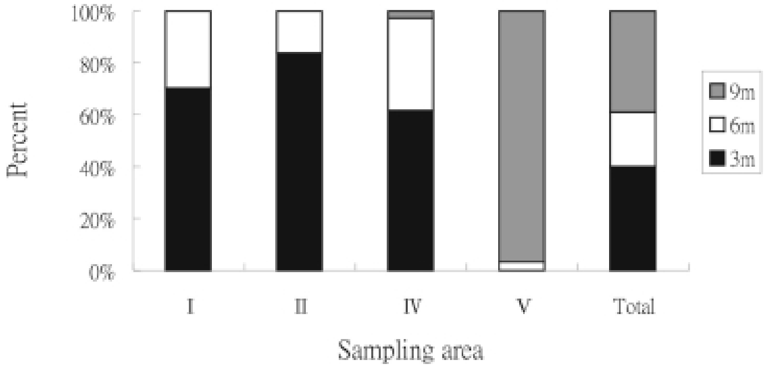


圖 3. 台灣東北部卯澳灣海域第二階段調查各小海區與三種深度所有海膽數量百分比。

Fig. 3. Percentage distribution of sea urchin by three depths (3, 6 and 9m) at the five sampling area in the Maoaw Bay of the northeastern Taiwan.

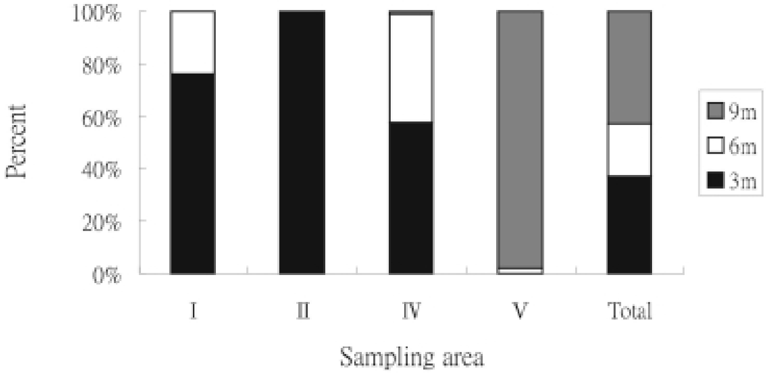


圖 4. 台灣東北部卯澳灣海域白尖紫叢海膽數量在各小海區與三種深度所占百分比。

Fig. 4. Percentages distribution of *Echinostrephus aciculatus* by three depths at the five sampling areas in the Maoaw Bay of the northeastern Taiwan.

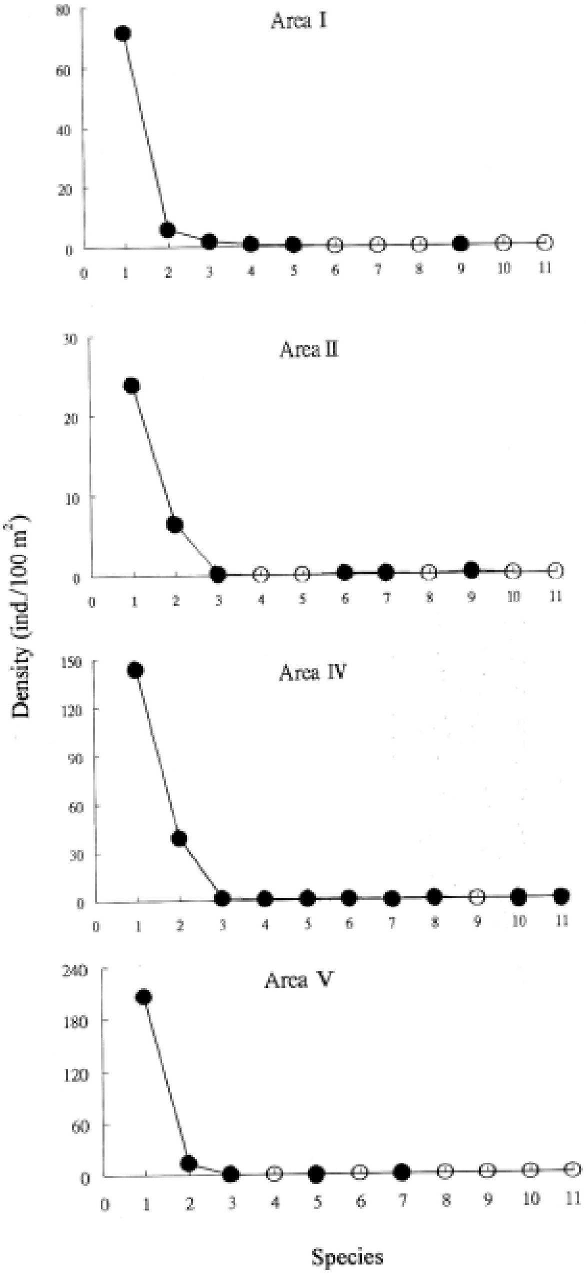


圖 5. 台灣東北部卯澳灣海域各種海膽各小海區之密度。實心圓表示有海膽，空心圓表示無海膽。

Fig. 5. Densities of sea urchins by species in the five sampling areas of the Maoaw Bay in the northeastern Taiwan (solid circles, present; open circles, absent; 1, *Echinostrephus aciculatus*; 2, *Echinometra mathaei*; 3, *Anthocidaris crassispina*; 4, *Echinostrephus molaris*; 5, *Stomopneustes variolaris*; 6, *Pionocidaris baculosa*; 7, *Diadema setosum*; 8, *Ecuidaris metularia*; 9, *Tripeustes gratilla*; 10, *Echinothrix calamaris*; 11, *Diadema sevignyi*).

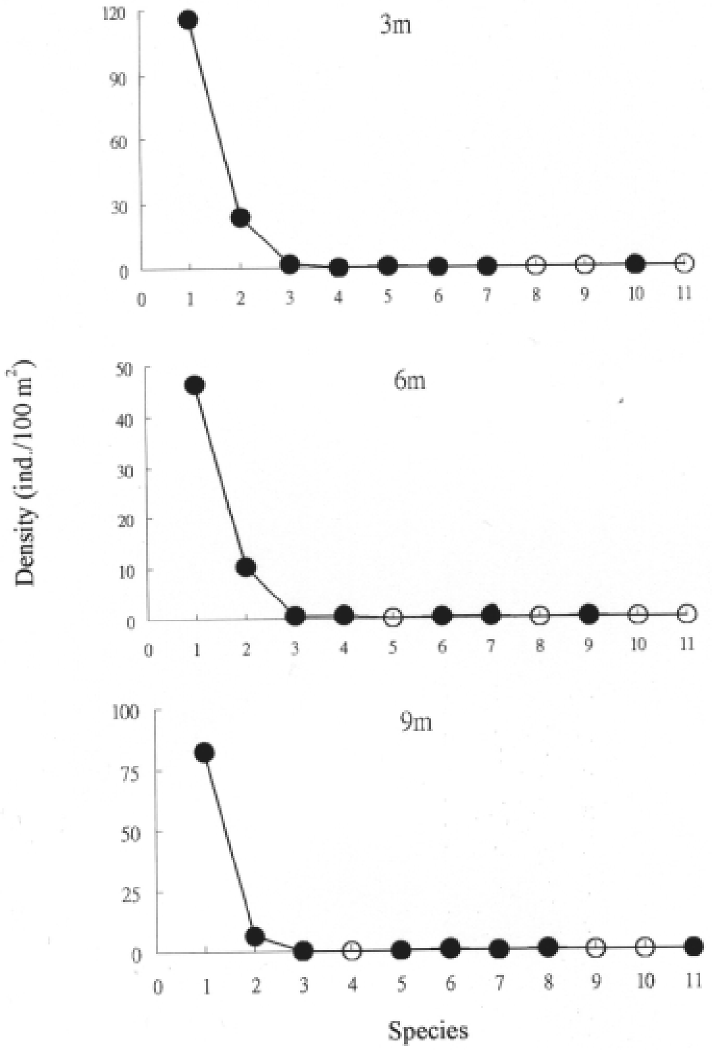


圖 6. 台灣東北部卯澳灣海域各種海膽各種深度之密度。實心圓表示有海膽，空心圓表示無海膽。

Fig. 6. Densities of sea urchins by depths in the Maoaw Bay of the northeastern Taiwan (solid circles, present; open circles, absent; 1, *Echinostrephus aciculatus*; 2, *Echinometra mathaei*; 3, *Anthocidaris crassispina*; 4, *Echinostrephus molaris*; 5, *Stomopneustes variolaris*; 6, *Pionocidaris baculosa*; 7, *Diadema setosum*; 8, *Ecuidaris metularia*; 9, *Tripeustes gratilla*; 10, *Echinothrix calamaris*; 11, *Diadema sevignyi*).

richness index均不高，以第IV區有最大值2.84，第V區有最小值1.51，Simpson's index以第II、IV區有最大值0.36，第V區有最小值0.12，Shannon's index以第IV區有最大值0.28，第V區有最小值0.12，Pielou's evenness index以第II區有最大值0.35，第V區有最小值0.17。但是四個歧異度指數在四個小海區間均無顯著差異(p>0.1) (表3)。

三種深度的Species richness index以9m有最大值2.64，6m有最小值2.20，Simpson's index以3m有最大值0.32，9m有最小值0.17，Shannon's index以3m、6m有最大值0.25，9m有最小值0.17，Pielou's evenness index以6m有最大值0.30，9m有最小值0.18。且四個歧異度指數值在三種深度間也均無顯著差異 (p>0.1) (表4)。

就整個海域來說，Species richness index (p＝ 0.08<0.1) 與 Simpson's index (p＝0.001<0.1) 指數值隨著優勢種白尖紫叢海膽的密度增加而呈遞減的趨勢 (圖 7)。

討 論

本調查中，4種歧異度指數值無論在小海區或深度均低，而且整個海域歧異度指數值也隨著優勢種白尖紫叢海膽密度增加呈現遞減趨勢，這些現象顯示本海域海膽種類會隨著海區、深度及底質不同呈現多樣性分布。

表 3. 台灣東北部卯澳灣海域各小海區之歧異度指數比較

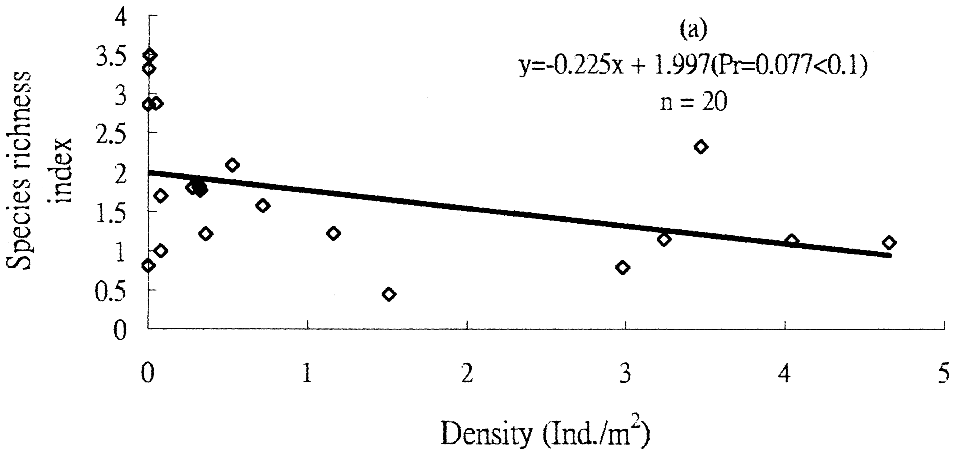
Table 3. Number of species and number of individuals collected, and estimated Species richness indices (d), Simpson's species diversity indices (c), Shannon's species diversity indices (H), and Pielou's evenness indices (e) of the sea urchins in the five sampling areas of the Maoaw Bay in the northeastern Taiwan

Sampling Area	Number of samples	Number of species	Number of individuals	*d*-value	*c*-value	*H*-value	*e*-value
I	9	6	723	1.75	0.20	0.20	0.26
II	8	6	248	2.09	0.36	0.27	0.35
IV	8	10	1490	2.84	0.36	0.28	0.28
V	2	5	440	1.51	0.12	0.12	0.17
Total	27	11	2901	2.88	0.29	0.26	0.24

表 4. 台灣東北部卯澳灣海域各深度之歧異度指數比較

Table 4. Number of species and number of individuals collected, and estimated Species richness indices (d), Simpson's species diversity indices (c), Shannon's species diversity indices (H), and Pielou's evenness indices (e) of the sea urchins in the three depths of the Maoaw Bay in the northeastern Taiwan

Depths (m)	Number of samples	Number of species	Number of individuals	*d*-value	*c*-value	*H*-value	*e*-value
3	14	9	1921	2.44	0.32	0.25	0.26
6	8	7	530	2.20	0.30	0.25	0.30
9	5	8	450	2.64	0.17	0.17	0.18
Total	27	11	2901	2.88	0.29	0.26	0.24



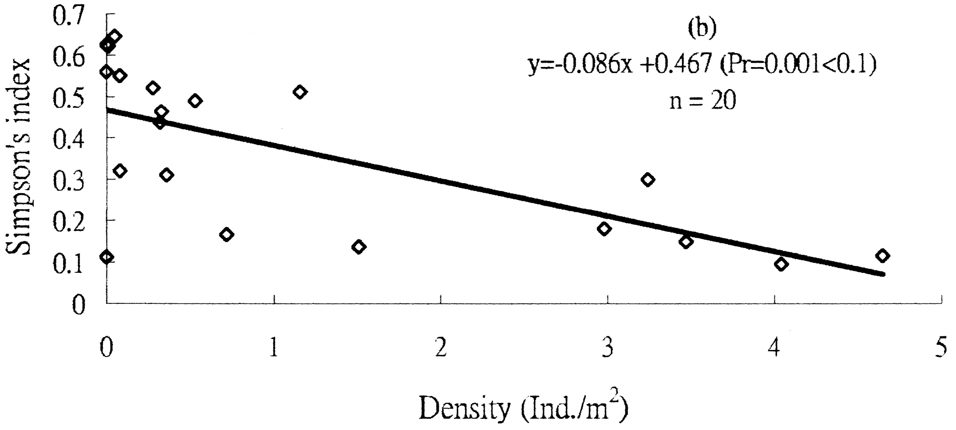


圖 7. 台灣東北部卯澳灣海域白尖紫叢海膽密度與歧異度指數的關係。(a) Species richness index，(b) Simpson's index。

Fig. 7. Relationships between the density of *Echinostrephus aciculatus* to the Species richness index (a) and to the Simpson's index (b) for sea urchins in the Maoaw Bay of the northeastern Taiwan.

台灣東北部海域由於地理位置特殊，除夏季之外，終年吹拂強勁東北風，海象惡劣，不易從事海上潛水調查工作，而本研究調查期間集中在夏季進行，因此目前尚無法探討本區海膽群聚結構是否存在季節差異。

本研究調查共記錄了5科11種的海膽，與之前的研究(鄭等 1994，1996，1997，1998)記錄6科14種接近。其中減少了冠海膽科(Diadematidae)的冠刺棘海膽(*Echinothrix diadema*)、刻肋海膽科(Temnopleurstidae)的芮氏刻肋海膽(*Temnopleurus reveesi*)，與毒棘海膽科(Toxopnerstidae)的喇叭毒棘海膽

(*Toxopneutes pileolus*)。此外，在本研究調查所有種類均爲正型海膽目，而無歪型海膽目的種類。其可能原因，或許是該海域原本就沒有歪型海膽種類棲息，或是因爲歪型海膽爲夜行性，且生活在沙地中(李及陳 1994)，導致目前的調查方法未能發現該目的種類。

在海膽的分布方面，本研究第一階段調查的結果發現海膽的密度，以平均水深6m處最高，3m次之，9m最低(表1)；而第二階段的調查結果，卻呈現水深3m密度最高，9m次之，6m最少的現象(圖 3)，二次調查的結果並不一致。其差異來源，主要是因爲第Ⅴ區存在數量眾多的海膽分布在9m的水深，而在第一階段的調查，深度僅止於水深7m左右。因此未來進行海膽數量調查時，深度至少應達9m以上，才能涵蓋海膽的棲息深度。

又在第二階段調查的結果中，第Ⅰ、Ⅱ、Ⅳ區海膽的密度在三種深度間，以3m處最高，6m次之，9m最少，其數量隨著深度的增加而遞減，但統計上並無顯著差異，其原因可能來自海膽呈塊狀分布，即使在同一深度內仍有很大的差異，使得三種深度密度間並無顯著差異存在。曾有研究指出夏威夷兩種海膽(*Echinometra* spp.)的分布和豐富度與水流及伴隨水流而來的藻類碎片有密切的關係，在水流較急促的地方，海膽的數量較豐富(Russo 1977)。本調查結果在3m水深處，由於水淺，受到海浪攪拌的影響較大，水流較強，藻類亦較容易破碎而漂浮在水中，或藻類的生物量較豐富，而較易爲海膽所攝食，唯隨著深度的增加，受到海浪的影響隨之遞減，而造成海膽數量在深度上也呈現相似的趨勢。這種數量隨著深度增加而減少的趨勢，也曾在地中海的海膽研究中被發現(Turon *et al*. 1995)。

另外，在卯澳灣外的第Ⅴ區，海膽大部分集中在9m的深度，推測其原因可能是本區海膽密度受海底底質的影響比水深來得重要。在第Ⅴ區海底底質主要爲大片礁岩平台所構成，礁岩隨著水深增加平緩下降，約在水深9m左右，礁岩呈現陡降分布。而本區海膽在水深6m以上較少被發現，而在水深9m左右，有許多的海膽分布在礁岩的垂直面上，而此微棲地分布上的差異可能是造成本區海膽的分布與其他第Ⅰ、Ⅱ、Ⅳ區有如此大的差異結果。

無論就整個海域或小海區或深度來看，種類間均是以白尖紫叢海膽的密度最高，是數量最多的優勢種類。若從小海區間的差異來看，則白尖紫叢海膽在第Ⅳ區的密度最高，第Ⅰ區次之，第Ⅴ區第三，第Ⅱ區最少，但是在統計上並無顯著差異(圖 5)。其原因在於該種類的分布爲塊狀分布，因此，縱使在某一小海區或某一深度內仍有很大的變異，使得統計檢定上無法顯出差異來。以往曾有研究以10m x 10m 的正方形採樣面積調查塊狀分布的海膽，並認爲此種大面積的採樣法可以改善採用穿越線法調查海膽的數量時，若穿越線恰好越過海膽群時，數量就高，反之數量就很低，可以因此降低採樣的誤差 (Moses and Bonem 2001)。然而若在本海域採用上述大面積樣區以進行調查，似乎也不太適合，因爲該海灣除了在第Ⅰ區地勢較爲平緩外，其他各小海區的地勢均很陡峭，因此若採用這種大面積調查法，反而很容易涵蓋到其他深度而造成另一個因子的誤差。爲了減小採樣誤差，或許只能藉由增加穿越線的重複數來達成，唯必須投入更多的人力、物力與時間。

本海區所計算的海膽歧異度指數，不論是在單一小海區或單一深度，其數值均不高，並且會隨著白尖紫叢海膽密度的增加，歧異度指數均呈現顯著的減少趨勢，顯示優勢種白尖紫叢海膽對該海域的海膽生物多樣性造成明顯地影響。在肯亞海域中的梅氏長海膽優勢種對冠海膽與藍環冠非優勢種的影

響也曾被提出過 (McClanahan 1988)。

海膽的豐度受掠食者影響很大(Carpenter 1981；Lewis 1986；McClanahan 1989，1995，1998；McClanahan and Muthiga 1989；Morrison 1988；Neudecker 1979；Pain 1966；Wellington 1982)。曾有研究指出，在未被保護而嚴重過漁的海域，海膽的密度約爲受保護海域的20倍，其原因爲人類的漁撈行爲使其主要掠食者數量減少所造成(Silva and McClanahan 2001)。海膽主要的掠食者包括有板機魨(Balistidae)、隆頭魚(Labridae)與龍占(Lethrinidae)，及一些無脊椎動物，如海星、頭足類等等(McClanahan 2000)。縱使在台灣過去並無關於海膽掠食者的調查研究，但是本海域優勢種白尖紫叢海膽的掠食者推測也應該包括這些魚類，這些掠食者魚類以往經常可以在漁船漁獲中被發現，但是在本調查的過程中卻不常發現到。此外，白尖紫叢海膽也具有在底質上挖出較本身軀體大2至3倍深的圓柱狀棲息洞穴，藉此躲避掠食者的攻擊(Russo 1980)。因此本研究推測本海域由於掠食者數量減少，再加上白尖紫叢海膽特有挖洞穴的生態習性，使其較能抵禦掠食者的攻擊，而得以成爲本海域的優勢種。

過去的調查指出白尖紫叢海膽、梅氏長海膽、環鋸棘頭帕海膽及白棘三列海膽是屬於豐富常見的種類，每次調查均可發現10隻以上，其餘種類則在10隻以下(鄭等 1994，1996，1997，1998)，但是在過去的調查中並無明確敘述所投入的努力量，如調查面積、人力與時間等有多少，因此無法與本研究直接作比較。在本研究中，除了白尖紫叢海膽與梅氏長海膽外，其餘9種海膽的密度均少於10隻/100m^2，數量均相當稀少，由於海膽是一種晝伏夜出的生物，到了晚上才開始覓食，而本調查進行的時間都在白天進行，可能造成某些種類數量的偏差。

具有經濟價值的種類，如白棘三列海膽(*Tripeustes gratilla*)、紫海膽(*Anthocidaris crassispina*)及口鰓海膽(*Stomopneustes variolaris*)，由當地漁民口述及調查(鄭等 1994，1996，1997，1998)得知該海域過去的數量相當豐富，只因人爲過度採捕造成目前數量稀少，因此，就物種的保育與資源管理利用而言，本海域的海膽資源值得未來投入更多心力加以維護。

未來將針對該海域優勢種白尖紫叢海膽進一步探討其族群調節的機制、競爭者、掠食者與微棲地的選擇，將有助了解海膽在底棲生態系所扮演的角色。

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以微隨體DNA研究粗首鱲（*Zacco pachycephalus*）的保育遺傳

Conservation Genetics of *Zacco pachycephalus* by Microsatellite DNA Locus Analyses

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摘要

粗首鱲是廣泛分布於台灣北部及西半部河川的特有種魚類，東部花東地區原本並沒有分布，現在花東地區溪流內的粗首鱲是人爲放流的結果。我們利用8個微隨體基因座(microsatellite loci)，對來自全省不同溪流的粗首鱲族群進行歸類分析(assignment analysis)，可以獲得97%的正確率，顯示不同溪流的粗首鱲間已有一定的分化，並可以微隨體基因座作爲分子標記，正確判別出粗首鱲個體的來源溪流。同樣對淡水河三大支流進行歸類，只有81%的正確率，顯示同一溪流中的次族群間遺傳分化不高，或者存在著頻繁的基因交流。以歸類分析追蹤東部的粗首鱲個體來源，發現東部的粗首鱲族群源自北部及中部溪流的多次放流。由粗首鱲的研究結果可知，利用微隨體基因座加上歸類分析方法，可有效地分析出淡水魚個體的可能來源，對保育工作尤其是淡水魚類保育及放流的管理而言，是很有用的工具。

Abstract

Zacco pachycephalus (Günther) is a common minnow endemic to freshwater streams in the northern and western Taiwan, and has been recently introduced to streams in the eastern Taiwan. We applied eight microsatellite DNA loci to make an assignment test to determine the genetic relationships of its populations among the streams with the success rate of 97%. This suggested that there was significant differentiation in the populations among the streams. When the assignment test was applied to individual fish from three tributaries of the Tamshui River, the success rate was 81%, indicating a low genetic differentiation among the populations in the same river. When the test was applied to the individual fish from the streams of the eastern Taiwan, it was able to identify their source populations in the northern and western Taiwan. Accordingly, the microsatellite DNA locus analysis is an effective method for determining genetic differentiation of stream fish and also for identifying source populations of introduced populations. The analysis is useful for conservation and management of freshwater fishes.

關鍵詞：粗首鱲、歸類分析、保育遺傳學、微隨體DNA

Key words : *Zacco pachycephalus*, assignment test, conservation genetics, microsatellite DNA

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緒言

溪哥是鯉科(Cyprinidae)鱲屬(*Zacco*)魚類的俗名，在台灣有兩個種：粗首鱲(*Zacco pachycephalus*)及平頜鱲(*Zacco platypus*)。粗首鱲爲台灣特有種，分布在台灣西部海拔1,200 m以下的淡水溪流，原本並未分布在台灣東部的溪流，然而近年來在東部溪流也發現粗首鱲的行蹤。平頜鱲廣泛分布於東亞沿海中海拔河段，包括中國大陸、日本及韓國，在台灣則侷限在北部的溪流(Wang *et al*. 1997; Wang *et al*. 1999)。粗首鱲與平頜鱲的外型極爲相似，皆爲流線形的體型，體長爲10-20 cm(最大可達30 cm)，體側有約10條的橫帶，成熟雄魚體色會轉爲泛紅，臀鰭變長延伸至尾鰭基部，嘴部出現追星。這兩種溪哥主要的不同點在於嘴裂的深度，粗首鱲嘴裂深度可達眼睛中線至眼睛後緣，平頜鱲嘴裂較淺，僅達眼睛前緣至1/3左右。由於兩種魚外型相似，在台灣統稱爲溪哥。外表形態雖然相似，但粗首鱲和平頜鱲在淡水河及雙溪共域，卻沒有見到大量的雜交個體，種間應有一定的生殖隔離產生。

粗首鱲以高屏溪爲界，可分爲兩個形態型，分別稱爲粗首鱲北型及粗首鱲南型(馬國欽 私人通訊)，兩型在外表形態上沒有明顯的差別，但在同功異構酶(allozyme)上有顯著的差異(Wang *et al*. 1999)。平頜鱲依據體側花紋也可分爲兩個形態型，分別稱爲平頜鱲台灣型及平頜鱲日本型(馬國欽 私人通訊)。平頜鱲台灣型體側花紋爲橫帶狀，外表形態類似中國大陸產的平頜鱲；平頜鱲日本型體側花紋呈片狀，與日本及韓國產的平頜鱲外形相似。依據釣魚人士的敘述，平頜鱲日本型最近幾年才出現在淡水河流域，且族群量有漸多的趨勢，顯示平頜鱲日本型個體可能非台灣的原生淡水魚。粒線體D-loop(馬國欽 私人通訊)與微隨體DNA(microsatellite DNA)(黃

2003)的研究也顯示，平頷鱲日本型的基因歧異度較台灣型高，且與日本的平頷鱲有相近的粒線體基因型，因此在台灣的日本型個體可能是日本平頷鱲經人爲放流而來。放流行爲對淡水魚族群的影響很大，淡水魚族群由於基因交流較少，多半呈現族群內基因歧異度不高但族群間分化程度甚高的狀況(Angers and Bernatchez 1998; Hedrick *et al*. 2001)，放流行爲相當於人爲加入外來族群個體，增加基因交流的頻率，對淡水魚族群的自然遺傳組成及結構會造成嚴重的影響。近年來，原本無溪哥分布的台灣東部溪流出現族群量不低的粗首鱲族群，即爲放流影響族群分布的明顯例證，而平頷鱲日本型的出現及擴張也顯示了外來族群對原生族群的影響。放流行爲的掌控及限制是必須的，要做好放流行爲的管控，必須能鑑定出外來的個體，並釐清個體的來源。

歸類分析(assignment test)可依據多個基因座(loci)的資料，計算個體來自不同族群的或然率，將個體歸類至可能的來源族群中。歸類分析廣泛的應用在族群遺傳研究、自然資源管理、保育遺傳研究以及法醫鑑定各方面(Davies *et al*. 1999; Eldridge *et al*. 2001; Roques *et al*. 1999)。常用的歸類分析方法包括貝氏分布方法(Bayesian method)、頻率決定方法(frequency method)及遺傳距離決定方法(distance method) (Cornuet *et al*. 1999; Rannala and Mountain 1997)。多型性越高的分子標記，能夠提供越高的解析力，常用來進行歸類分析的分子資料有同功異構酶、RFLP (restriction fragment length polymorphism)、RAPD (random amplified polymorphic DNA)及微隨體DNA (Davies *et al*. 1999)。

微隨體(microsatellite)是基因體中常見的片段，由1-6 bp大小的重複單元重複5-100次組成，由眞菌到脊椎動物，幾乎所有生物的基因體內皆有微隨體DNA的出現。微隨體在基因體中的含量豐富，變異性高，屬於共顯性遺傳且多爲中性演化，這些特點使它成爲族群遺傳、遺傳疾病、親屬關係鑑定等研究的重要工具(Goldstein and Schlotterer 2000)。一般作爲分子標記的微隨體序列包含兩個部分：重複序列(repeat sequences)以及兩端非重複的序列(flanking regions)。由基因體中選殖出微隨體基因座後，自兩端非重複序列部分設計適當的引子，即可利用這些引子自基因體中以PCR技術放大出微隨體基因，並判讀個體的基因型。一個個體的基因型包含兩個對偶子，且不同對偶子間的差異主要是來自重複次數的不同，因此取PCR產物進行電泳分離即可判讀出個體的基因型。

微隨體DNA多型性很高，能作到個體層次的判別(Waits *et al*. 2001)，因此本研究利用微隨體基因座的資料，對不同族群的粗首鱲個體進行歸類分析，檢驗不同溪流中個體的基因差異程度，並建立一套有效的方法，對未知來源的個體加以鑑定。

材料與方法

一、 樣本採集

以垂釣的方式在全省各地12個流域共採得302條粗首鱲(表1)，採得之魚體在解剖後立即取下內臟及肌肉組織，置於液態氮中保存，或者置於70%酒精中收藏於-20℃。由於我們詳細分析淡水河三條支流新店溪、基隆河和大漢溪的族群，所以大多數的樣本來自這三條河流，在其餘的河川進行代表性的採樣，而不一一分析流域內的細節。

二、 DNA的萃取

取30 mg的保存於低溫酒精中的組織，剪碎放進1.5 ml的離心管中，以1 ml的STE buffer洗三次後加入150 μl的lysis buffer及300 μg的proteinase K，55℃水浴兩小時以

表1. 採樣地點和樣本數

Table 1. Sampling localities and sample sizes

Drainage & abbreviation	River or locality	Sample size
Tamsui River (TS)	Luofu Bridge (Shihmen Reservior)	6
	Pinglin	2
	Jinggualiao River	4
	Gupoliao River	3
	Sanshuitan	7
	Kuolai	13
	Wulai	11
	Xinxian	3
	Tonghou River (upper reach)	13
	Tonghou River (lower reach)	25
	Zhongyangxincun (down from Bitan)	11
	Bitan (up from Bitan)	13
	Gunagxing (Pingguang River)	14
	Shuangshikou	13
	Badu	1
	Ruifang	9
	Houtong	13
	Dongshige	9
Houlong River (HL)	Sheliaojiao	10
Dadu River (DD)	Puli	10
Putzu River (PZ)	Niuchou River	10
Tzenwen River (TW)	Nanhua Reservoir	6
Kaoping River (KP)	Sandimen	9
	Ailiao River	10
Fangshan River (FS)	Fangshan River	9
Lanyang River (LY)	Lanyang River	10
Hsiukuluan River (SKL)	Chungling Primary School	12
	Zhuoxi	10
Lichia River (LC)	Lichia River	12
Chihpen River (CP)	Chihpen River	12
Taimali River (TML)	Connecting cannel	12
Total		302

上，再加入150 μg的RNase A水浴30分鐘，然後以phenol/chloroform的萃取法(Sambrook *et al.* 1989)進行DNA萃取，最後加入1 ml的95%酒精將DNA沉澱出來。沉澱出來的DNA以70%的酒精清洗兩次以去除鹽類，接著以真空離心的方式將酒精抽乾，將得到的DNA沉澱物溶至0.1X TE buffer中，儲藏於-20℃。

三、 PCR引子

我們自粗首鱲基因體中篩選出的8個微隨體基因座，並設計出引子(黃 2003)。引子的序列及基因座的基本特徵列於表2。

四、聚合酶連鎖反應(Polymerase Chain Reaction)

以標記有螢光物質FAM, HEX，或TAMRA的引子進行聚合酶連鎖反應。反應物包括50-200 ng樣本DNA、1X *Tag* polymerase buffer、0.4-1.2 μl $MgCl_2$ (25 mg)、0.4-0.8 μl dNTP (2.5 mM)、0.1-0.3 μl primers (10 μM)、0.5U *Tag* polymerase (Promega)，補水至總體積爲10 μl。將反應物放置於溫度控制器(PTC-100，MJ RESERCH)中進行反應，反應流程如下：95℃ 5分鐘；95℃ 30秒，黏合溫度 30秒，72℃ 30-40秒，重複25-30次；72℃ 10分鐘。

五、 基因型判讀

將PCR反應產物置於96孔盤中，以酒精沉澱方式進行純化，純化後的產物加入

表2. 八個微隨體基因座的基本資料(Ta:引子的最佳黏合溫度; H_O:異型合子觀測值; H_E:異型合子期望值)

Table 2. General characters of 8 microsatellite loci for *Z. pachycephalus* (Ta: annealing temperature; H_O: observed heterozygosity; H_E: expected heterozygosity)

Locus	Repeat motif	Primer sequences	Ta(℃)	H_O	H_E
Z128A	$(GT)_{14}$	L 5'-TGCCTGATGACTCACTGCTT R 5'-CGTACACCTTCAGCTCTCTGC	64	0.457	0.749
ZD181	$(GA)_{18}$	L 5'-GTCAGTCAGACCCTCACACT R 5'-CATTTTGTTTGTCACAGTCG	60	0.550	0.753
ZD366	$(GT)_5AT(GT)_8(GA)_5(n)_{43}(GT)_{15}$	L 5'-GTTTTTCTAGTCCTCGTTCC R 5'-GCAGTCATGTCATATTTCCG	60	0.778	0.883
ZD992	$(CT)_{12}$	L 5'-CTCGCTCATATTTCTACCCA R 5'-ATTTTCCACAGTTTTGACGC	60	0.646	0.770
ZD1021	$(GT)_{15}$	L 5'-GATGATGATGGGATAGATGC R 5'-TGGGAATCAAACTACAGAGC	60	0.553	0.742
ZD582	$(GT)_{13}$	L 5'-ACTTTCTGTGTGTGTATAAATGC R 5'-GTGTTATTGTGCCTTGTGG	60	0.477	0.642
ZD331	$(GT)_3GC(GT)_{16}(GA)_7$	L 5'-CAACACAATCACCATCCCCT R 5'-CAACGCATTACAACCTCTCTG	60	0.675	0.827
ZD657	$(CA)_6(TC)_8(TA)_{22}$	L 5'-AATGACCTTGGTTGTGTAGC R 5'-AACAGGCATAAAGTGAATAGAGA	60	0.695	0.868

loading solution及ET-400標記(Amersham)作產物分子大小判讀依據，以MegaBASE 500自動定序儀及Genetic profiler 2.0軟體(Amersham)判讀其基因型。每條魚的基因型判讀結果見黃(2003)。自動定序基因型的圖譜存於台大動物所的資料庫中，歡迎有興趣者連絡通訊作者借用參考。

六、 哈溫平衡的檢測

若族群中的個體符合自由交配，且族群量夠大，可以忽略選汰壓力及突變的影響時，族群中的基因型頻率會維持一個特定的比例，我們稱這種狀態爲哈溫平衡(Hardy-Weinberg equilibrium) (Hartl 2000)。歸類分析方法假設族群處於哈溫平衡狀態。利用GENEPOP程式(Raymond and Rousset 1995) (http://www.cefe.cnrs-mop.fr/)，以Fisher's exact test檢測不同的基因座-族群對是否符合哈溫平衡。

七、 F_{ST}的計算

在本研究中，使用 *F* statistics (Weir and Cockerham 1984)無偏估值中的F_{ST}值作爲族群的分化指數。

Weir and Cockerham(1984)提出的無偏估值，是以對偶子頻率求得變方後，再以此變方來估算族群內對偶子的相似度及遺傳結構。將族群內的均方(mean square)期望值分爲三個部分：族群間(δ^2_P)、族群內(δ^2_I)及對偶子間(δ^2_G)。而代表不同層次的族群結構係數公式爲：

$$F_{IT} = (\delta^2_P + \delta^2_I)/(\delta^2_P + \delta^2_I + \delta^2_G)$$

$$F_{ST} = \delta^2_P /(\delta^2_P + \delta^2_I + \delta^2_G)$$

$$F_{IS} = \delta^2_I /(\delta^2_I + \delta^2_G)$$

F_{ST}的估算由MSA程式計算，並利用1000次的random permutation進行顯著性的檢定。此檢定將基因型資料作隨機的置換，以模擬無族群分化的狀態，每次的重新置換都可求出新的F_{ST}值，將此數值與觀測值作比對，計算模擬數值大於或等於觀測值的比例，即爲支持族群無分化假說的比例。

八、 歸類分析

利用電腦軟體GENECLASS (Cornuet *et al*. 1999)，以Bayesian方法進行歸類分析(Rannala and Mountain 1997)。過去的研究顯示，Bayesian method的正確率是所有歸類分析方法中最高的(Cornuet *et al*. 1999)，且族群的分化程度越高(F_{ST}值越大)，歸類的正確率會越高，若要分析F_{ST}值大於0.3的族群，只需使用5個基因座及各族群10個樣本，即可達到將近100%的正確率(Cornuet *et al*. 1999)。Bayesian方法假設族群符合哈溫平衡，且基因座間處於連鎖平衡，此時在j基因座中基因型k/k'出現的機率在族群i的機率會等於

$[(n_{ijk}+1)/(K_j+1)][(n_{ijk}+1)/K_j]/(n_{ij}+2)(n_{ij}+1)$；

若k=k' (即同型合子的情況)

$2[(n_{ijk}+1)/K_j]\ [(n_{ijk'}+1)/K_j]/(n_{ij}+2)(n_{ij}+1)$；

若k≠k'(即異型合子的情況)

n_{ijk}及$n_{ijk'}$：在族群i中，基因座j對偶子k及k'的個數

n_{ij}：在族群i中，基因座j所含對偶子總和，族群數爲n者，其n_{ij}爲2n

K_j：在所有族群中，基因座j所含對偶子之種類

利用上列式子估算出個體出現於某族群的機率之後，以兩個方式判定個體可能的來源族群：(一)直接歸類。認定或然率最高的族群爲個體的來源族群。(二)排除式歸類。以模擬1000次的方式檢驗個體來自某一族群的可能性，個體若是出現在此族群的可能性小於顯著水準，就代表該族群不可能是個體的來源族群。以此方式排除不可能的族群，未排除之族群即爲可能的來源族群。因此個體可被歸類至不只一個族群，也可能無法歸類爲任一族群。此方式旨在免除第二類的錯誤，採用的顯著水

準越高，嚴苛度也越高(例如，5%之顯著水準的嚴苛度高於1%)。

結果

一、哈溫平衡的檢測

哈溫平衡檢測結果顯示，粗首鱲8x12組基因座/族群的組別中，多數組別(96%, 92組)符合哈溫平衡(p<0.05)。因此，我們可以使用這8個基因座進行歸類分析。

二、F_{ST}值的計算

以八個微隨體基因座的資料計算台灣粗首鱲族群間F_{ST}值。全省12個族群兩兩間的F_{ST}值，最小爲0.064(大肚溪vs.朴子溪)，最大爲0.562(利嘉溪vs.枋山溪)，總平均爲0.244，詳細列表於表3。而顯著性檢測顯示，12個族群間皆有明顯的分化(p=0.001)。

三、歸類分析的正確率

對全省12條溪流及淡水河3條支流的粗首鱲個體使用直接歸類分析，所使用的基因座數目與歸類正確率之間的關係如圖1(基因座依照對偶子的數目，由高到低依序加入)，正確率隨著所使用的基因座數目增加而上升。在全省溪流的歸類中，使用8個基因座的正確率爲97%。在淡水河三大支流的歸類部分正確率較低，只有81%。

四、直接歸類分析

(一) 全省12個粗首鱲族群：歸類分析結果如表4(a)。302條粗首鱲中，只有8個個體被誤判至其他溪流，正確率爲97%。誤判個體中，4個個體來自淡水河，分別被誤歸爲大肚溪(1個體)、秀姑巒溪(2個體)及利嘉溪(1個體)；2個來自大肚溪，分別被誤歸爲後龍溪

表3. 全省12個粗首鱲族群間的F_{ST}值以及p值 (族群代號如表1)

Table 3. Population fixation index (above the diagonal) and the p value (below the diagonal) based on permutation test for all pairwise combinations of 12 *Z. pachycephalus* populations (population abbreviations are the same as in Table 1)

	TS	HL	DD	PZ	TW	KP	FS	LY	SKL	LC	CP	TML
TS		0.236	0.257	0.303	0.280	0.271	0.459	0.177	0.097	0.221	0.211	0.281
HL	0.001		0.101	0.153	0.138	0.188	0.477	0.203	0.166	0.136	0.135	0.210
DD	0.001	0.001		0.064	0.118	0.173	0.447	0.278	0.182	0.174	0.096	0.177
PZ	0.001	0.001	0.001		0.109	0.163	0.454	0.289	0.219	0.246	0.139	0.211
TW	0.001	0.001	0.001	0.001		0.139	0.485	0.270	0.225	0.255	0.170	0.274
KP	0.001	0.001	0.001	0.001	0.001		0.331	0.272	0.225	0.247	0.220	0.282
FS	0.001	0.001	0.001	0.001	0.001	0.001		0.562	0.470	0.533	0.497	0.555
LY	0.001	0.001	0.001	0.001	0.001	0.001	0.001		0.191	0.239	0.233	0.250
SKL	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001		0.164	0.114	0.254
LC	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001		0.098	0.179
CP	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001		0.126
TML	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	0.001	

表4. 歸類分析結果 (族群代號如表1)

Table 4. Results of the assignment tests for *Z. pachycephalus* (population abbreviations are the same as in Table 1)

(a) 全省12個族群的歸類分析結果(表內數字代表個體數)

(a) Self-classification of individuals in 12 populations (number of individuals)

		Original population											
		TS	HL	DD	PZ	TW	KP	FS	LY	SKL	LC	CP	TML
Reference population	TS	166											
	HL		10	1									
	DD	1		8									
	PZ				10								
	TW			1		6							
	KP						19						
	FS							9					
	LY								10				
	SKL	2								22			
	LC	1									11		1
	CP											12	
	TML										1		11

(b) 淡水河三大支流的歸類分析結果

(b) Self-classification of individuals in 3 tributaries of Tamsui River

		Original population		
		DH	HT	KL
Reference population	DH	4	10	1
	HT	2	111	8
	KL		11	23

(c) 東部族群個體歸類至西部族群的分析結果

(c) The individuals in eastern populations assigned to other populations

		Original population			
		SKL	LC	CP	TML
Reference population	TS	13	1	1	
	HL	2			
	DD	5	10	10	10
	PZ				2
	TW				
	KP				
	FS				
	LY	2	1	1	

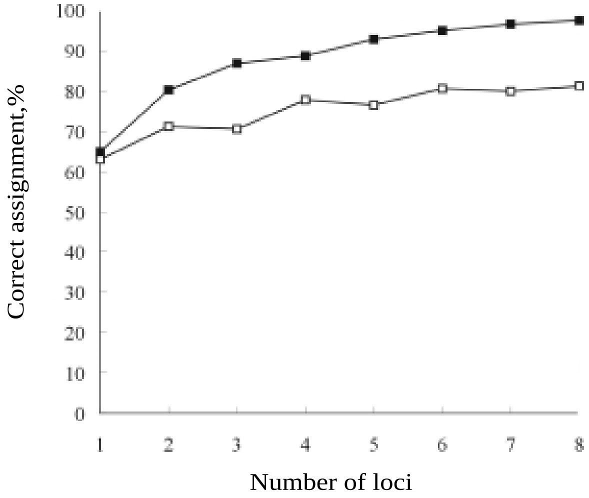

圖1. 歸類分析的正確率與所使用微隨體基因座數目的關係。

Fig. 1. Relationships between the percent correct assignment and number of loci for 12 drainages (solid squares) and the Tamsui River (open squares) of Taiwan.

及曾文溪；還有1個來自於利嘉溪被誤歸爲太麻里溪，以及1個來自太麻里溪誤歸爲利嘉溪。

(二) 淡水河三大支流：對淡水河的粗首鱲作歸類分析，結果如表4(b)。共170個個體中，有32個個體被誤歸，正確率爲81%。大漢溪6個個體中有2個個體被誤歸至新店溪；新店溪132個個體中有10個被誤歸至大漢溪，11個被誤歸至基隆河；基隆河32個個體中，有8個被誤歸至新店溪，1個被誤歸至大漢溪。

五、 排除式歸類

(一) 全省12個粗首鱲族群：以模擬的方式模擬個體可能出現在不同族群內的機率，並以5%的顯著水準作檢驗。在5%的顯著水準之下，個體可被正確歸類回來源族群(出現於其他族群的可能性均小於顯著水準者)的比例爲62.9%。

(二) 淡水河三大支流：以模擬方式進行分析，在5%的顯著水準之下，個體可正確歸類回來源族群的比例爲11.2%。大部分的個體都被歸類至兩個以上的族群，且以直接歸類方式進行歸類，正確率也在90%以下，故使用這8個微隨體基因座，無法對淡水河不同支流中的個體作正確歸類。

六、 東部族群的來源

東部族群係人工放流而來，以直接歸類法分析東部溪流中溪哥可能的放流來源。分析結果如表4(c)。秀姑巒溪的22個粗首鱲樣本有13個可歸類至淡水河，5個個體可歸類至大肚溪，另外2個個體歸類至後龍溪，2個個體歸類至蘭陽溪。利嘉溪和知本溪的12個個體中，各有10個個體可歸類至大肚溪，1個個體歸類至淡水河，還有1個個體歸類至蘭陽溪。太麻里溪12個個體中，有10個個體可歸類至大肚溪，另外2個個體歸類至朴子溪。

討　論

歸類分析的正確率與所使用的基因座數目及族群間的分化程度相關，所使用的基因座數目越多，族群間的分化程度越高，歸類分析的正確率越高。以8個微隨體基因座對全省分布的粗首鱲進行分析，歸類的正確率高達97%，顯示粗首鱲以流域爲界，微隨體基因型有明顯的區分，不同溪流族群間已有一定的分化，利用8個微隨體基因座，即可有效的分辨個體來自哪一個溪流。以同樣的方式分析淡水河流域中三大支流中的粗首鱲個體，正確率只有81%。此現象可能因爲三支流間分隔產生的時間不長，或者是基因交流頻繁所導致。由於新店溪、基隆河及大漢溪在下游的匯流處，因鹽度過高及污染因素，並沒有粗首鱲的分布(馬國欽 私人通訊)，這三個支流間若有基因交流頻繁的現象，可能是洪水將個體帶到匯流處，或者是頻繁的人爲放流所導致。

利用微隨體基因型判讀加上歸類分析方法，我們可以有效的判別未知個體的來源，研究族群間基因交流的概況，並推測外來個體的可能起源。東部的粗首鱲族群是近年來才出現的，針對東部的粗首鱲個體進行歸類分析，追溯其可能的來源。分析結果顯示，放流來源主要是淡水河及大肚溪，但也有些個體來自北部及中部其他的溪流。由此推測，東部的粗首鱲族群可能是多次放流的結果。值得注意的是，並沒有任何個體被歸類至南部的高屏溪及枋山溪族群，東部溪流的放流來源來自北部和中部，皆屬於粗首鱲北型。

以高變異度的分子標記加上歸類分析方法，可以有效的鑑定出個體的來源，操作容易且準確性高。除了可鑑定外來個體的來源外，在漁業資源管理上，可利用歸類分析方法，鑑定所捕獲魚隻的來源地，以掌控不同魚群(stock)的資源概況(Roques *et al*. 1999)，野生動物資源也可利用類似的方式進行管理。而在保育遺傳研究方面，也可利用歸類分析方法，研究族群間的相互遷移行爲，評估外來個體侵入造成的影響(Davies *et al*. 1999; Eldridge *et al*. 2001)，以對不同族群間的人爲放流行爲作適當的管理與限制。

然而歸類分析的前提是必須有原始族群基因頻率的基礎資料，故我們建議對台灣境內淡水魚類建立基本的遺傳資料是目前保育遺傳措施的第一要務。

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合歡山區泰雅晏蜓卵期與稚蟲期之發育

Egg and Larval Developments of the Taiyal Darner *Aeshna petalura taiyal* Asahina (Odonata, Aeshnidae) at the Mt. Hohuan

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摘要

泰雅晏蜓(*Aeshna petalura taiyal* Asahina)爲台灣特有亞種，廣泛分布於1,500m以上高山地區。稚蟲棲地高山湖沼受到人爲開發、水質污染與魚類放生干擾，族群現況頗受關注，故於1997-2000年對合歡山區泰雅晏蜓卵期與稚蟲期之發育進行研究。結果顯示雌蜓於夏末產卵，卵以發育遲緩現象越冬後於翌年春季孵化，卵期接近10個月。稚蟲期世代數隨二樣區之不同，各爲1年1代或2年1代。由於泰雅晏蜓卵與稚蟲期相當長且利用棲地包括水域與週邊陸域，相當容易受人爲活動干擾影響，故整體湖沼的保護仍是泰雅晏蜓保育之重要關鍵。

Abstract

The Taiyal darner *Aeshna petalura taiyal* Asahina, 1938 is an endemic subspecies of dragonfly in Taiwan. It occurs widely in the mountain areas above 1,500m in elevation. Its larval habitat has been adversely affected by human activities, such as pond construction, water pollution, and fish releasing. This study was conducted between 1997-2000 to study egg and larval developments of the Taiyal darner in the Mt. Hohuan area. The results showed that the period of egg stage was about ten months. Eggs were laid at the end of summer, overwintered in a diapause condition, and hatched in the following spring. The larval voltinism showed univoltine or semivoltine at the two different sampling sites of the study area. The egg and larval stages were fairly long, and its habitat consisted of both aquatic and terrestrial environments, easily disturbed by human activities. For conservation of the Taiyal darner, it is recommended to protect whole lake and its adjacent environments.

關鍵詞：泰雅晏蜓、卵、稚蟲發育、合歡山、湖沼

Key words: *Aeshna petalura taiyal*, egg, larval development, Mt. Hohuan, lake

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緒言

泰雅晏蜓*Aeshna petalura taiyal* Asahina屬蜻蛉目(Odonata)、晏蜓科(Aeshnidae)、晏蜓屬(*Aeshna*)、藍晏蜓群(Cyanea group)，爲朝比奈正二郎在台灣北部高山採集命名的新種晏蜓(Asahina 1938)，該文對於終齡稚蟲的形態特徵、體型大小已有相當詳細描述。其後Asahina採納Erich Schmidt意見並參考台灣產泰雅晏蜓與產於東喜瑪拉雅之原名亞種在體表斑紋、雌蜓肛附器(caudal appendages)之形態差異與地理隔離分布，修訂爲台灣地理亞種(Asahina 1983)。本亞種爲台灣分布於最高海拔的蜻蜓類，成蟲採集紀錄皆於海拔1,500m以上地區(Lieftinck *et al*. 1984)；相關生態僅有簡單描述，如羽化過程有若干失敗死亡比例(Ishida and Hamada 1973)；雌蜓產卵於近水邊且有短草覆蓋之土地(Asahina 1983)；湖沼中有不同發育階段稚蟲(Lieftinck *et al*. 1984)；稚蟲生活在山地且週圍有樹蔭的小池沼(Matsuki and Lien 1991)。

近年泰雅晏蜓稚蟲棲地高山湖沼受到人爲開發與魚類不當放生，棲地品質逐漸劣化，族群現況實需加以注意(朱耀沂 私人通訊)。由於卵與稚蟲期生活史是蜻蜓保育行動必需收集的重要資料(Matsuki 1997)，因此本研究選定合歡山區進行泰雅晏蜓野外發育調查，其目標爲調查卵形態、胚胎、稚蟲發育及羽化期等，並依研究結果對泰雅晏蜓保育提出建議。

材料與方法

合歡山區位於台中、南投、花蓮縣交界處，在太魯閣國家公園範圍內。本區年雨量平均在3,000 mm以上，年平均溫度在6℃以下，平均相對溼度80%以上，屬於低溫重溼型氣候；山區植被型除少數山峰爲玉山圓柏(*Juniperus squamata*)及杜鵑灌叢盤據外，其餘3,000m以上地區則爲台灣冷杉(*Abies kawakamii*)及玉山箭竹(*Yushamia niitakayamensis*)的鑲嵌狀分布(林及賴 1994)。

因本區位高山平夷面，湖沼頗多，爲避免研究項目相互干擾，故於不同湖沼進行卵與稚蟲期發育調查(圖1)。卵期調查樣區爲東峰圓池(Station(St.)1)(24° 8'3"N, 121° 16'45"E, 3,100m in elevation)，本池位於合歡山莊東面下方約200m處，略呈圓形，面積約100 m^2。池水約呈黃褐色，底部富含有機質。湖岸週圍爲開闊箭竹草原，湖濱著生多種苔蘚爲蟲卵棲地。稚蟲調查樣區爲東峰長池(St.2)(24° 8'36"N, 121° 16'45"E, 3,090m)與石門池

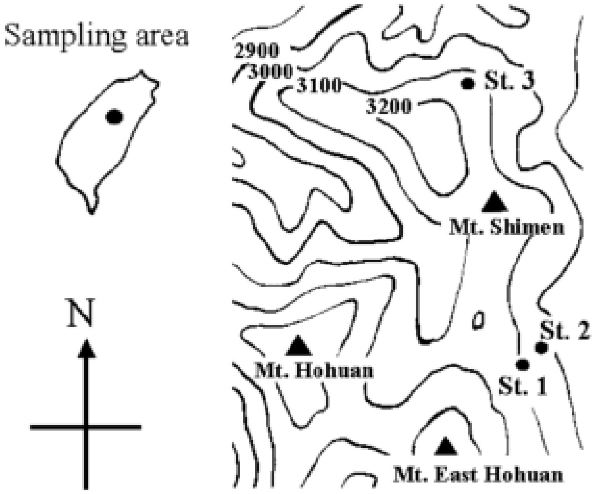

圖1. 合歡山樣區與採樣站相關位置圖(St. 1 東峰圓池；St. 2東峰長池；St. 3石門池)。

Fig. 1. Sampling stations (Sts. 1-3) in the Mt. Hohuan area.

(St. 3) (24° 9'48"N, 121° 16'24"E, 3,100m)。東峰長池(St. 2)在東峰圓池(St. 1)下方約10m處之長形池，面積約100 ㎡，平均深度45 cm，池水約黃褐至黑褐色，底質有機物亦豐。石門池(St. 3)位石門山北方約1 km處，爲道路施工堰塞合歡溪上游之長方形水池，面積約65 ㎡，平均深度40 cm，水色呈綠色至黃色，底質以軟泥及碎石爲主，有機質較少。

由於泰雅晏蜓雌蜓以產卵器將卵埋入苔蘚等介質而產卵，無法肉眼觀察到蟲卵位置，且人工介質誘導產卵並未成功，惟此蟲數量少，故僅犧牲雌蜓一隻並取出腹部第7至8節蟲卵於解剖顯微鏡下測量、攝影並描述。

1998年1月至1999年12月，每月於東峰圓池(St. 1)苔蘚較多之東、南、西岸各取10 cm ×10 cm苔蘚一塊。將苔蘚攜回並肉眼揀出所有蟲卵，於解剖顯微鏡下挑除破裂或變形死卵，再以解剖針剔除卵殼觀察發育。參考Ando (1991)及Miyakawa (1990)將胚胎發育分爲5期，表徵如下：第I期爲胚胎發育陷入(anatrepsis)而眼點尚未出現；第II期爲眼點出現後至胚胎脫出(katatrepsis)運動前；第III期爲胚胎正處於脫出運動中；第IV期爲胚胎完成脫出，但體背仍爲無胚部分；第V期爲胚胎已完全背合(dorsal closure)，但尚未孵出。由蟲卵數量與胚胎發育變化探討整年發生情形。

1997年7月至1999年6月於東峰長池(St. 2)及石門池(St. 3)，每月1人以框長30 cm、寬16 cm、網目大小1.5 mm之D型手抄水網各撈取稚蟲1小時，將撈出稚蟲以游標尺測量頭寬後釋回，由於頭寬大小可代表稚蟲齡期，故稚蟲族群的頭寬分布變動將可用於探討其形態變化與發育成長。比較不同樣區稚蟲一年世代數差別，並沿岸收集羽化蛻殼估計羽化期。於稚蟲活動之池塘底部以酒精溫度計、CYBERSCAN酸鹼度計、HACH-CO150導電度計及CONSORT-Z521溶氧量計測量湖心底層水溫、導電度(conductivity)及溶氧量(dissolved oxygen)，另取表水攜回實驗室以

HACH DR/2000光電比色計組合測定濁度(turbidity)、總氮量(total Kjeldahl nitrogen)及總磷量(total phosphorus)，統計水質因子平均值並以Wilcoxon符號等級測驗(Wilcoxon's signed rank test)比較二樣區水質差異。

結果與討論

一、卵期

解剖所取之卵呈長紡錘形，卵長1.81 ± 0.08 mm，寬0.41 ± 0.02 mm(n=8, mean ± S.D.)，在紡錘形較細端之頂端有一凸起圓錐狀精孔(micropyles)。卵外觀爲淡褐色，外表光滑無膠層(jelly layer)等物附著(圖2)。

圖3表示東峰圓池(St.1)樣區泰雅晏蜓蟲卵調查量與胚胎發育期變化。1998年1至3月間之胚胎以第II期爲主，至3月第IV期胚胎明顯增加，4與5月則以第V期胚胎爲主。6、7月未發現蟲卵，至8月再度發現蟲卵並皆爲第I期，9月則包括第I、II期，10月至翌年2月皆以第II期爲主。2月後發育加快，第II期占51%，第IV期占37%。3月第IV期占26%，第V期占2%。4至6月之間皆爲第V期，至6月僅發現1處於第V期胚胎之卵。7月無蟲卵，8月後蟲卵又復出現亦以第I期爲主，9月亦包括第I、II期，10至11月以第II期爲主，12月第II、IV約各占一半。由卵胚胎發育變化推測，雌蜓產卵期約於8月開始，於秋季胚胎迅速發育，冬季發育較遲緩，過冬後又恢復發育速度，翌年春季大部分蟲卵已發育成熟並於初夏前孵化，卵期接近10個月。

Corbet (1999)歸納蜻蛉目昆蟲胚胎發育分爲三型：第一型爲產卵後胚胎在適溫下直接發育孵化(direct development)，第二型爲胚胎在冬季低溫期有一段發育遲滯期，待回昇適溫後胚胎再行發育與孵化，屬於遲延發育型(delayed development)，第三型爲蟲卵兼具第一型與第二型胚胎發育之兼性遲延發育型(facultative diapause)，即部分蟲卵在冬季低溫期前即孵出，但也有部分蟲卵可越冬後再孵出。由於蜻蛉目早期稚蟲易受低溫危害，故以卵期越冬將比以早期稚蟲越冬更有生存優勢(Sternberg 1995)。在本調查中，泰雅晏蜓蟲卵絕大部分在胚胎脫出運動期前，即進入過冬之發育遲緩期，待翌年春季再度快速發育與孵出，雖然有零星泰雅晏蜓蟲卵在冬季前即發育至第IV期或第V期，但由本文後述之稚蟲發育調查，冬季前並未調查到任何早

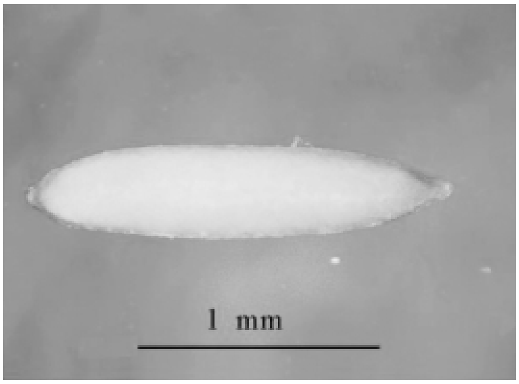

圖2. 泰雅晏蜓蟲卵。

Fig. 2. An egg of *Aeshna petalura taiyal*.

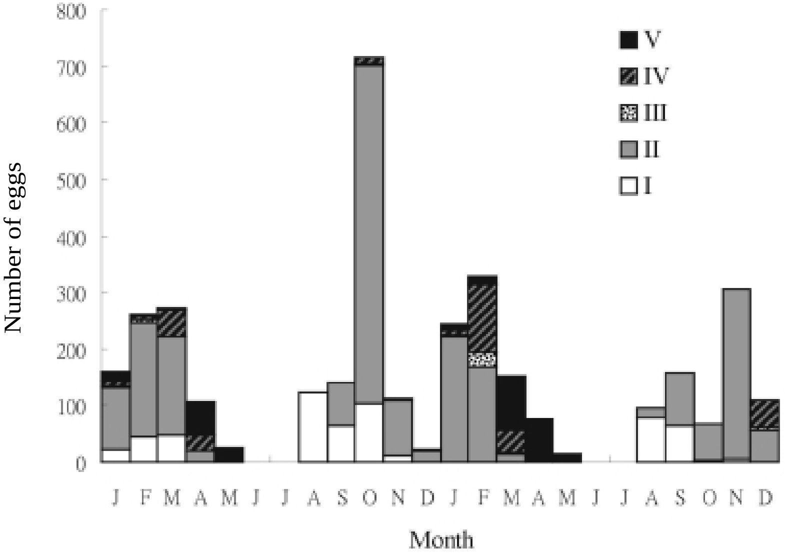

圖3. 1998年1月至1999年12月東峰圓池(St. 1)各月之蟲卵胚期 (I-V)組成。

Fig. 3. Monthly composition of the embryonic developmental stages (I-V) of *A. p. taiyal* at St. 1 from January 1998 to December 1999.

期稚蟲，早期稚蟲皆在翌年6至8月出現，由此可知在秋末直接發育孵出者，早期稚蟲可能無法渡過冬季低溫期，故整體胚胎發育過程較接近第二型之胚胎遲延發育類型。

二、稚蟲期

東峰長池(St. 2)與石門池(St. 3)水質項目平均值如表1，除水溫無顯著差異(Wilcoxon's signed rank test, *p*＞0.05)，酸鹼度、導電度、溶氧量、濁度、總氮量及總磷量有相當顯著差異(Wilcoxon's signed rank test, *p*<0.01)。即石門池酸鹼度、導電度與溶氧量高於東峰長池，總氮量、總磷量與濁度遠低於東峰長池。石門池為天然河道因修築道路堰塞而成，由岩層湧出的泉水包含較多礦物質，所以有較高導電度與弱鹼性水質。由於此人工池沼形成時間不長，底質仍以沙泥為主，故水中有機物堆積不多，水質較為澄清潔淨。東峰長池則在箭竹草原上，可能是冰斗所形成的天然池沼，受到箭竹枯枝落葉等長期持續堆積，池底有機質相當豐富，湖水也有較多的腐植質懸浮，故濁度、總氮量、總磷量相當高，水質較為污濁，一般稱此類水色的池沼為咖啡池或紅茶池。但因二池沼平均深度皆未達50 cm，池水溫度易受氣溫與風擾動影響，致使二者在水溫上並無顯著差異。

東峰長池(St. 2)共測量稚蟲1,184隻次，頭寬分布具5明顯峰度(圖4)，終齡稚蟲 (F0)頭寬最大峰度值在8.7-8.8 mm，終齡前1、2、3、4齡稚蟲(F1、F2、F3、F4)各為7.1-7.4、5.9-6.0、4.9-5.0、4.1-4.2 mm。稚蟲調查量與頭寬分布見圖5，在1999年6月已出現頭寬小於0.20 cm小型稚蟲，6至10月間稚蟲頭寬分布有明顯變動增大，但在11月至翌年2月頭寬分布則無太大變動，至3至6月頭寬分布又具有明顯變動增大至終齡稚蟲的頭寬大小。由

表1. 東峰長池(St. 2)與石門池(St. 3)之水質比較 (n=24)

Table 1. Physicochemical variables (mean ± standard error, n=24) at St. 2 and St. 3

	St. 2	St. 3	*p**
Temperature (℃)	16.4 ± 1.0	16.8 ± 1.0	＞0.05
pH	6.2 ± 0.1	8.4 ± 0.1	＜0.01
Dissolved oxygen (mg/l)	5.6 ± 0.5	8.5 ± 0.4	＜0.01
Conductivity (μ mho/cm)	7.6 ± 1.3	102.9 ± 3.7	＜0.01
Turbidity (FTU)	133 ± 18	17.0 ± 3.0	＜0.01
Total Kjeldahl nitrogen (mg/l)	7.1 ± 0.5	3.8 ± 0.2	＜0.01
Total phosphorus (mg/l)	1.3 ± 0.2	0.3 ± 0.0	＜0.01

＊Wilcoxon signed rank tests, significant levels : *p*＜0.01, significant at 1%; *p*＞0.05, non significant.

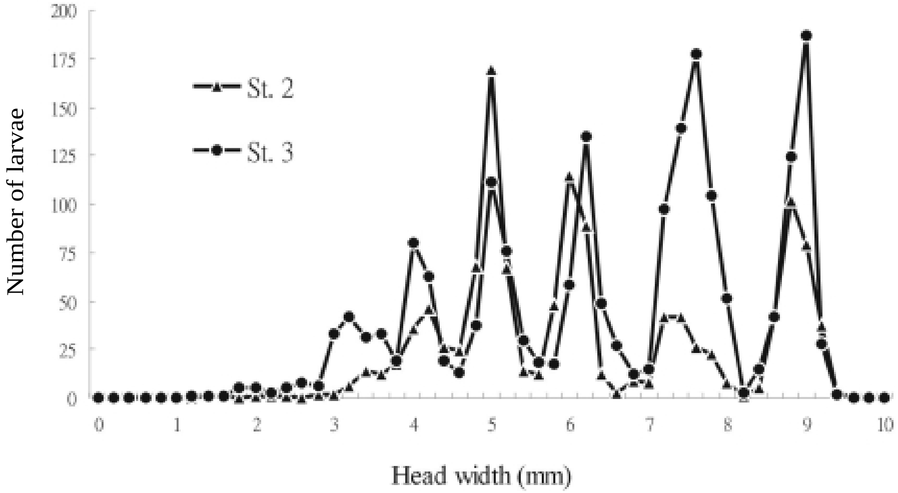

圖4. 東峰長池(St. 2)與石門池(St. 3)所有稚蟲頭寬調查值之分布。

Fig. 4. Frequency distributions of *A. p. taiyal* head width of larvae based on the pooled data at St. 2 and St. 3.

1997年新加入同生群(cohort)稚蟲頭寬分布，逐月變動所呈現的一年一波形，從此可知該晏蜓稚蟲生活史以1年1代爲主，在1998年新加入同生群亦有1年1代爲主的相同現象。由於調查期間每月皆在東峰長池樣區發現頭寬大於0.85 cm終齡稚蟲，本樣區仍有不明顯的世代重疊現象。

石門池(St. 3)測量稚蟲1,921隻次，頭寬分布亦有5明顯峰度(圖4)，F0、F1、F2、F3、F4最大峰度值爲8.9-9.0、7.5-7.6、6.1-6.2、4.9-5.0、3.9-4.0 mm，與東峰長池(St. 2)之峰度分布疊合相當一致，即二樣區後期齡蟲大小應無異。石門池小型稚蟲亦於調查年間的6至8月出現，終齡稚蟲亦終年有之。本

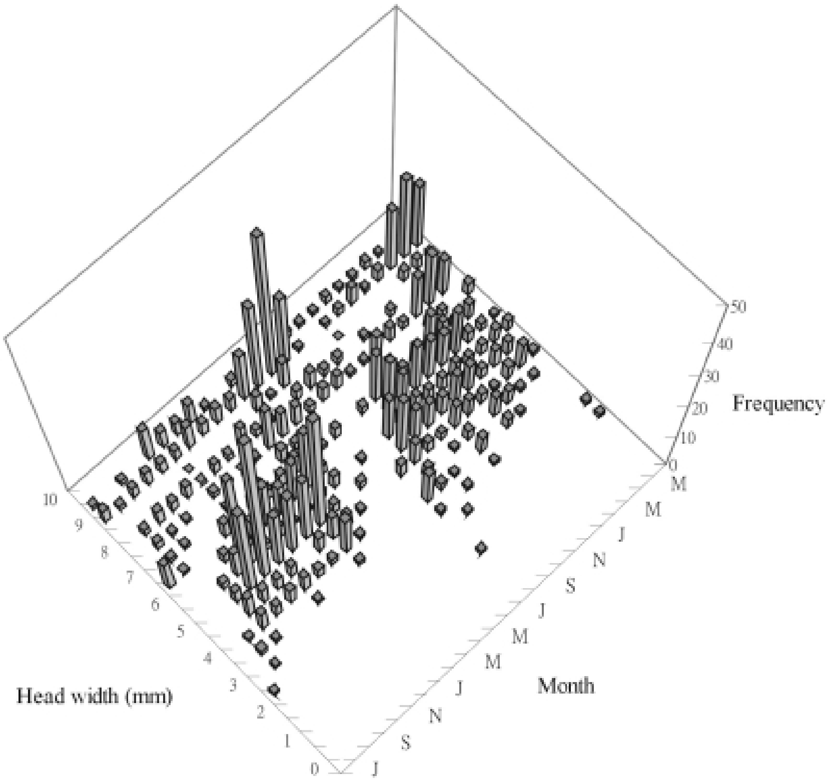

圖5. 1997年7月至1999年6月東峰長池(St. 2)稚蟲之頭寬頻度分布。

Fig. 5. Frequency distribution of head width of *A. p. taiyal* larvae in relation to months at St. 2 from July 1997 to June 1999.

樣區稚蟲世代重疊現象非常明顯，頭寬逐月變化無明顯波形(圖6)，由1997年7月新加入同生群頭寬分布逐月變化，稚蟲一般經兩年才成爲終齡稚蟲，如此以兩年完成一代之稚蟲期生活史。

綜言之，二樣區小型稚蟲皆於夏季出現，稚蟲於溫暖季節有較快的生長速度，冬季低溫期則發育相當遲緩。稚蟲期生活史視不同樣區呈現以1或2年爲主，並於調查年間的5至9月羽化(圖7)。

蜻蜓稚蟲爲適應不同環境，生活史長短與世代數各有差異，影響因素包括季節、緯度、海拔、溫度與食物量等(Danks 1991; Krishnaraj and Pritchard 1995)，亦有高的環境溫度加速稚蟲生長並降低齡期間生長比例使成蟲體型較小的報導(Pickup and Thompson 1990; Hayashi 1990)。但由二樣區水溫無顯著差異，且稚蟲秋末至初春皆呈現發育相當遲緩現象，推測稚蟲生活史長短受到水溫以外因素影響。由二樣區終齡至終齡前4齡稚蟲(F0-F4)體型無明顯差別顯示，即使世代數不同，但至少稚蟲期後半段之後期齡蟲體型大小並無差別，推論後期齡蟲需成長至適當大小才能進行蛻皮，而成長速度差異影響體型大小，進而影響蛻皮，故使二樣區稚蟲生活史長短因而不同。東峰長池所含氮、磷等有

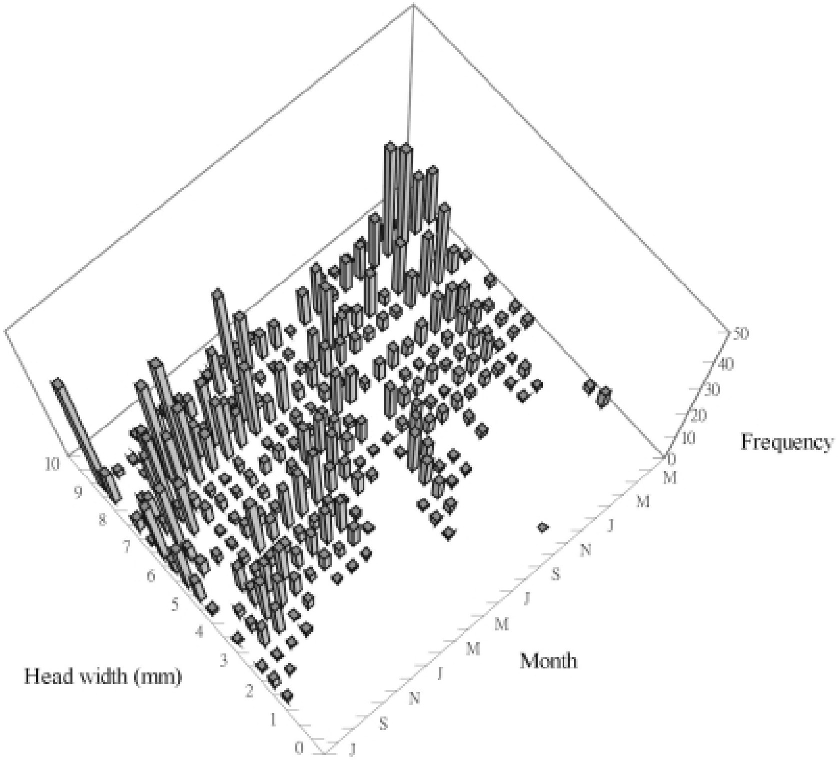

圖6. 1997年7月至1999年6月石門池(St. 3)稚蟲之頭寬頻度分布。

Fig. 6. Frequency distribution of head width of *A. p. taiyal* larvae in relation to months at St. 3 from July 1997 to June 1999.

機物質較石門池高，由現場觀察其底質有機碎屑與搖蚊等食餌量亦較豐，推測食物量可能是造成本研究中稚蟲成長速度與世代數差異主因，惟其機制爲何仍待後續實驗探討。

三、保育建議

Lieftinck *et al*. (1984)報導泰雅晏蜓成蟲採集紀錄皆於海拔1,500m以上地區，林(1997)報導稚蟲採集地紀錄皆在2,000m以上，如小雪山天池(2,530m)、阿里山姐妹潭(2,100m)、七彩湖(2,900m)、溪南山池(2,600m)等。由於泰雅晏蜓蟲卵胚胎一般需經冬季發育遲緩階段，在較低海拔環境溫度將使胚胎直接發育孵出，使早期稚蟲面臨冬季低溫危害，故蟲卵胚胎發育有較嚴格的溫度需求。此氣候條件可能使稚蟲生育地更侷限於高山地區，其生育地分布範圍應較前人認知爲小，族群分布仍需持續關注。

卵期調查中所採集到的主要苔蘚種類包括曲尾苔(*Dicranum* sp.)、棉苔(*Plagiothecium nemorale*) 與折葉蘚(*Diplophyllum* sp.)等，林(1991)報導此三種皆屬於玉山地區箭竹林下未受人爲干擾的濱溪系種類，且棉苔爲水生地帶之指標物種，故本調查地點亦爲相當濕潤的天然環境。苔蘚往往有很強吸水力與減緩水分喪失結構，適應水分間歇供應，因此在泰雅晏蜓卵期接近10個月期間，苔蘚可提供較適合的潮溼環境。由於溫度、水分及遮蔽

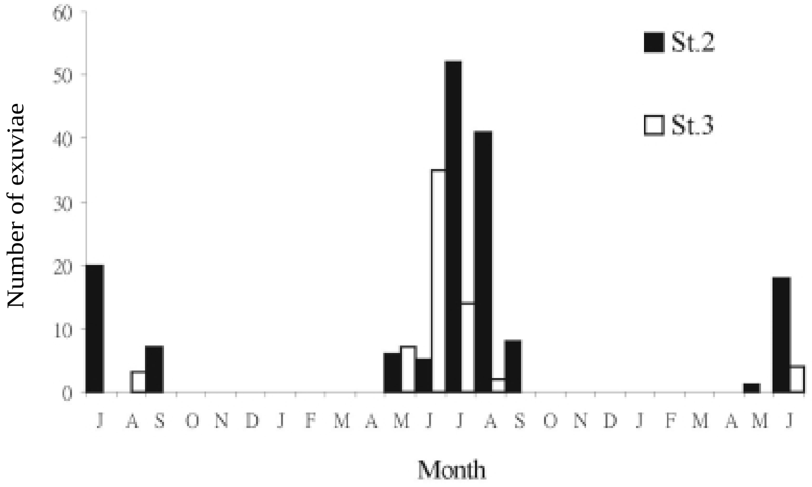

圖7. 1997年7月至1999年6月東峰長池(St. 2)與石門池(St. 3)羽化蛻殼調查量。

Fig. 7. Number of exuviae of *A. p. taiyal* collected at St. 2 and St. 3 from July 1997 to June 1999.

物等對蜻蜓胚胎存活與發育速度有顯著影響(Michiels and Dhondt 1990)，因此池岸水泥化建築將對泰雅晏蜓有很大的衝擊，建議湖泊管理單位應維持湖岸自然景觀，如有工程施作需要應保留相當的天然棲地，並以兼顧環境保護與物種保育的工法施工。

兩個稚蟲調查樣區除泰雅晏蜓稚蟲外，其他大型底棲動物僅包括沼石蛾(*Limnephilus* sp.)、豆龍蝨(*Agabus fulvipennis*)與搖紋科(Chironomidae)幼蟲，其群聚組成相當簡單。泰雅晏蜓稚蟲體型大且爲肉食性，在調查期間兩個樣區皆相當容易採到多量的稚蟲，故其生態地位相當優勢。雖然合歡山區在目前並無放生魚類干擾，但在台灣其他局部地區的高山湖沼，經筆者野外調查正面臨因宗教或遊憩需要而人爲放生魚類，如鯉魚(*Cyprinus carpio*)、鯽魚(*Carassius auratus*)與泥鰍(*Misgurnus anguillicaudatus*)的強烈干擾。McPeek(1990a, 1990b)指出某些蜻蛉目稚蟲對於魚類並不具有避敵行爲的適應性，若遭魚類入侵將致使該水域的族群滅絕。因此建議湖泊管理單位應有效禁止民眾錯誤放生魚類的行爲，如果發現放生魚類時，應以網具或對環境衝擊較小的藥物等方法清除魚類，恢復泰雅晏蜓稚蟲棲地，以利永續生存。

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Altitudinal Differences in Temporal Distribution, Spatial Preference and Timing of Breeding Climax of Frogs and Toads in the Central Taiwan

台灣中部蛙類與蟾蜍在時間分布、空間偏好與生殖高峰的海拔差異

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Abstract

This study compared temporal niche breadth, temporal niche overlap, spatial preference, and timing of breeding climax of frogs and toads in Wushikeng at 1,000m in elevation and in Chichi at 240m in the central Taiwan. The results showed that a species that had a wider temporal niche tended to have a wider niche overlap with other species. Also, the temporal niche breadths of the frogs and toads were significantly correlated with their temporal niche overlaps, while both niche breadths and overlaps were wider at the high elevation than at the low elevation. Most of the species expressed a spatial preference to either land or stream, but some showed no preference. An exception was *Rana latouchii*, which preferred land at the high elevation but stream at the low elevation. This was perhaps due to difference in water availability (precipitation) between the two elevations. The timing of breeding climax of most of the species at the high elevation was about two months later than that at the low elevation, except for *Buergeria robustus* the timing was the same at both elevations.

摘　要

本研究選擇台灣中部地區海拔1,000m之烏石坑與海拔240m之集集，比較兩地蛙類與蟾蜍的時間生態區位寬度、時間生態區位重疊度、空間偏好及生殖高峰期的海拔差異。結果顯示：一物種若有較寬之時間生態區位，該物種與其共棲物種間也將擁有較大的生態區位重疊度。此外，時

間生態區位寬度與時間生態區位重疊度呈現顯著性相關，且隨著烏石坑到集集海拔高度的降低，其寬度與重疊度亦下降。大部分物種在群聚中會表現出物種對空間偏好的特殊性，其選擇可以是陸域、溪流或沒有偏好。在此兩海拔物種空間偏好方面，唯一例外的是拉都希氏赤蛙，該蛙在烏石坑偏好出現在陸域，而在集集則偏好在溪流。其原因可能由於兩地海拔差異導致雨水的可利用性(降雨量)不同所致。在烏石坑大部分蛙類的生殖高峰比集集約晚2個月，只有褐樹蛙例外，該蛙在兩地擁有相同的生殖高峰。

Key words: amphibian, altitudinal differences, niche breadth, niche overlap, spatial preference

關鍵詞：兩棲類、海拔差異、生態區位寬度、生態區位重疊度、空間偏好

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Introduction

Animals tend to occupy wide ranges of temporal and spatial niches to maximize their resource utilization and to reduce interspecific competition. These niches differ among species, and are expressed by difference in their temporal appearance and/or spatial distribution (Begon *et al*. 1990). Frogs are poikilothermic animals and have physiological and behavioral adaptation to surrounding environments, causing the occurrence of altitudinal variation in temporal appearance, breeding period, and life history in many species (Pettus and Angleton 1967; Beattie 1985, 1987; Miaud *et al*. 1999; Lai *et al*. 2003). Also, the adult stage of frogs consists of the land phase for growth and the water phase for reproduction, coinciding with the seasonal changes in their surrounding environments. Different species of frogs usually choose different habitats for foraging, resting, and reproduction (Gao 1994; Chu 1996).

The purpose of this study was to determine interspecific and intraspecific differences in temporal and spatial niche utilization of frogs and toads, in terms of temporal niche breadth, temporal niche overlap, spatial preference, and the timing of breeding climax between two elevations: 1,000m in Wushikeng and 240m in Chichi in the central Taiwan.

Materials and Methods

Study stations

Two study stations representing two different elevations and temperature regimes were established: one in Wushikeng (24° 16' N, 120° 56' E) at an elevation of 1,000m and the other in Chichi (23° 51' N, 120° 44' E) at 240m (Fig. 1). The Wushikeng Station was located in the Central Mountain Range and covered with artificial coniferous and broad-leaf forests. The Chichi Station was located in the peripheral hills of the Central Mountain Range, and was an area

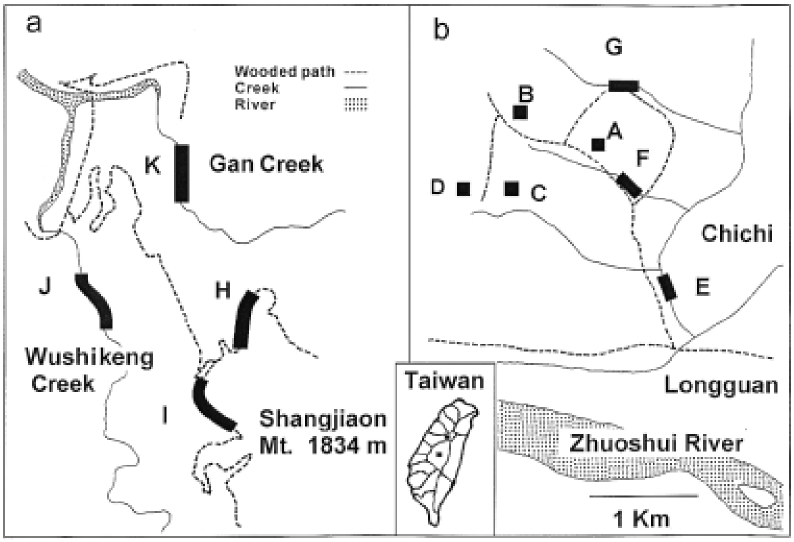

Fig. 1. The land sustations (A-D and H-I) and stream substations (E-G and J-K) at the Wushikeng Station (a) and the Chichi Station (b).

surrounded by working and abandoned orchards.

At each of the two stations, we designed land substation and stream substation for the study to represent, respectively, the habitat for land feeding phase and for stream breeding phase of frogs. The two substations at each station had the same size in the total area but differed in shape (design) due to different topography and stream conditions. At the Wushikeng Station, four 500m x 4m transects were established: two for each of the two substations (Fig. 1a). For the stream substation, one transect was along the bank of Wushikeng Creek and the other along Gan Creek. Both creeks had running water all the year round. Each of the two transects of the land substation was set in the mountain slopes of each of the creeks, where small, permanent and temporary pools were sparsely distributed. At the Chichi station, three transects, each 50m x 6m, were established along three small streams as the stream substation. These streams had flowing water in spring and summer, but was dry in fall and winter except after heavy rain. Four 15m x 15m plots encircling a small permanent pool were established as the land substation (Fig. 1b).

Survey method

Field surveys were conducted bimonthly from February 1997 to December 1998 at the Wushikeng Station, and from February 2000 to December 2001 at the Chichi Station. For each survey the visual encounter method (Heyer *et al.* 1994) was used to record the species and the number of adult frogs observed. Breeding behavior, including mating and spawning, was noted to determine the breeding period. The month with the highest numbers of mating individuals observed in the breeding period for a species was treated as the breeding climax for that particular species. The surveys were conducted one hour after sunset to reduce the influence of illumination.

Data analyses

Numbers of adult frogs of each species counted at each substation in the same month were summed up for two successive years as the relative abundance of the species for that month at that particular substation. The seasonal pattern in abundance was compared among species. In this study we regarded abundance of each species of frogs in different investigated months as its temporal niches, and abundance in difference between land and stream habitats as its spatial niches.

The temporal niche breadth that expresses the scope of utilizing a temporal resource by a species was measured by the following formula (Levins 1968):

$$B_i = 1/\sum_{j=1}^{n} P_{ij}^2 \text{..} (1)$$

where B_i is niche breadth of species i; P_{ij} is the proportion of species i found in month j (j = 1 to 6, representing February to December) of the survey period.

The temporal niche overlap that expresses a degree of overlap in a temporal resource between two species was measured by the following formula (Pianka 1973):

$$\alpha_{yx} = \left(\sum_{j=1}^{n} P_{xj}{*}P_{yj}\right) / \sqrt{\sum_{j=1}^{n} P_{xj}^2 {*} \sum_{j=1}^{n} P_{yj}^2} \text{...........} (2)$$

where α_{yx} is niche overlap between species x and species y; $P_{xj(\text{or } yj)}$ is proportion of x (or y) species found in month j in the survey period. The α_{yx}-value is a symmetric measure of overlapping, so that an overlap of species x to species y is identical to the overlap of species y to species x. It ranges from 0 (no overlap: no temporal niche shared in common by species x and species y) to 1 (100% overlap: the same temporal niche share by species x and species y).

The proportion of total individuals of each species was compared between the land and stream substations by the *Chi-square* test to determine the homogeneity of individual distributions within and between the two substations. The spatial preference of each species was then defined as the species with terrestrial, aquatic or no preference.

Meteorological data

The mean monthly air temperatures from February 1997 to December 1998 and February 2000 to December 2001 were obtained from the Wushikeng meteorological station for the Wushikeng Station and from the Endemic Species Research Institute in Chichi for the Chichi Station. The annual average temperature at Wushikeng was 18.5℃ (range from 12.5℃ to 23.2℃), that was 4.4℃ lower than 22.9℃ (range from 17.0℃ to 27.8℃) at Chichi (Fig. 2).

Results

Temporal niche breadth

At the Wushikeng Station 11 species were found, and 6 species had sufficient data for calculating B_i-values, whereas at the Chichi Station 16 species were found, and 12 species were calculated for the B_i-values (Table 1). The species diversity and abundance were higher at the Chichi Station than those at the Wushikeng Station.

At Wushikeng, *Bufo bankorensis* had the widest temporal niche breadth with the B_i-value of 5.53, whereas *Rana sauteri* had the narrowest value of 2.14. At Chichi the widest B_i-value was

Table 1. Temporal niche breadths (B_i-values) calculated for each species of frogs and toads based on the number of individuals counted at the Wushikeng Station, 1997-1998 and at the Chichi Station, 2000-2001 (total numbers of individuals observed in parentheses)

Species	Wushikeng	Chichi
Bufo bankorensis	5.53 (488)	1.55 (52)
Rhacophorus moltrechti	4.53 (76)	3.32 (146)
Buergeria robustus	3.44 (109)	3.50 (81)
Rana sauteri	2.14 (67)	1.50 (298)
Rana latouchii	4.70 (135)	3.56 (595)
Rana swinhoana	4.27 (150)	
Polypedates megacephalus	* (5)	3.25 (143)
Chirixalus eiffingeri	* (6)	3.76 (67)
Buergeria japonicus	* (3)	* (6)
Rana kuhlii	* (2)	* (2)
Chirixalus idiootocus	* (5)	
Bufo melanosticus		5.10 (53)
Rana limnocharis		3.55 (23)
Rana guentheri		3.90 (38)
Microhyla ornata		2.74 (35)
Microhyla heymonsi		2.31 (19)
Rana rugulosa		* (1)
Micryletta steinegeri		* (1)

* Numbers too small to calculate B_i-values.

for *Bufo melanosticus* at 5.10 and the narrowest value was for *R. sauteri* at 1.50 (Table 1). Five species whose B_i-values were measured were found at both Wushikeng and Chichi stations. Four of them had wider values at Wushikeng than those at Chichi. They were *B. bankorensis*, *R. sauteri*, *Rana latouchii*, and *Rana swinhoana*, whereas *Buergeria robustus* had fairly similar values between the two stations.

Temporal niche overlap

The niche overlaps expressed by α_{yx}-values were compared among the six species, of which B_i-values were calculated for the Wushikeng Station. The α_{yx}-value was highest (0.98) between *Rhacophorus moltrechti* and *R. latouchii*, and lowest (0.15) between *Rh. moltrechti* and *R. sauteri* at Wushikeng (Table 2). The average α_{yx}-values (Table 2) and the B_i-values at Wushikeng (Table 1) were significantly correlated (r-value =0.93, df=5, p<0.01).

A similar relationship in niche overlap was also found at Chichi (Table 3). Among 12 species with B_i-values (Table 1), the α_{yx}-value

Table 2. Niche overlaps (α_{yx}-values) among different species of adult frogs and toads at the Wushikeng Station

Species	1	2	3	4	5	6	Average
1 *Bufo bankorensis*	-	0.79	0.56	0.71	0.81	0.72	0.72
2 *Rhacophorus moltrechti*		-	0.77	0.15	0.98	0.77	0.69
3 *Buergeria robustus*			-	0.16	0.78	0.77	0.61
4 *Rana sauteri*				-	0.20	0.35	0.31
5 *Rana latouchii*					-	0.71	0.70
6 *Rana swinhoana*						-	0.66

was highest (1.00) between *Polypedates megacephalus* and *B. robustus*, and lowest (0.04) between *R. sauteri* and *Microhyla heymonsi* (or *Microhyla ornata*). Like the case at Wushikeng, the average α_{yx}-values (Table 3) were also significantly correlated with the B_i-values at Chichi (Table 1) (r-value =0.73, df=11, p<0.01).

Spatial preference

At the Wushikeng Station, the number of individuals observed at the stream substation was significantly higher than at the land substation for *B. bankorensis*, *B. robustus*, *R. sauteri and R. swinhoana*, suggesting that these four species preferred the stream habitat to the land habitat (Table 4). In contrast, *Rh. moltrechti* and *R. latouchii* prefered land to stream. At the Chichi Station *Rh. moltrechti*, *P. megacephalus*, *M. ornata and M. heymonsi* preferred land to stream, whereas *B. bankorensis*, *B. robustus*, *R. sauteri* and *R. latouchii* preferred stream to land. *Chirxalus eiffingeri*, *B. melanosticus*, *Rana limnocharis* and *Rana guentheri* showed no special preference to either land or stream (Table 4).

Breeding climax

The months of breeding climax of five species of frogs and toads observed at both two stations are shown in Table 5. The peak breeding seasons of *B. bankorensis*, *Rh. moltrechti*, *R. sauteri* and *R. latouchii* at Wushikeng were two months later than those at Chichi. An exception was that *B. robustus* had the same breeding climax season at both stations.

Discussion

Temporal niche breadth

Levins (1968) proposes that niche breadth be estimated by measuring the uniformity of distribution of individuals among the resource states. Niche breadth scores can be used to designate species as a generalist with a wide tolerance to environments or a specialist with a narrow tolerance to the environment (Dash and Mahanta 1993).

In this study *B. bankorensis* had the widest temporal niche breadth at the Wushikeng Station but not at the Chichi Station (Table 1). This species is widely distributed in the Central Mountain Range and is observed at elevations

Table 3. Niche overlaps (α_{yx} -values) among different species of adult frogs and toads at the Chichi Station

Species	1	2	3	4	5	6	7	8	9	10	11	12	Average
1 Bufo bankorensis	-	0.81	0.16	0.29	0.82	0.14	0.16	0.33	0.11	0.19	0.12	0.05	0.29
2 Rhacophorus moltrechti		-	0.25	0.35	0.93	0.24	0.22	0.47	0.28	0.27	0.22	0.13	0.38
3 Buergeria robustus			-	0.10	0.36	1.00	0.98	0.89	0.91	0.91	0.91	0.89	0.67
4 Rana sauteri				-	0.62	0.06	0.10	0.18	0.20	0.13	0.04	0.04	0.19
5 Rnan latouchii					-	0.33	0.32	0.53	0.41	0.35	0.30	0.25	0.47
6 Polypedates megacephalus						-	0.99	0.91	0.90	0.94	0.93	0.88	0.67
7 Chirixalus eiffingeri							-	0.93	0.90	0.97	0.95	0.90	0.67
8 Bufo melanosticus								-	0.92	0.96	0.96	0.88	0.72
9 Rnan limnocharis									-	0.87	0.95	0.97	0.68
10 Rana guentheri										-	0.95	0.86	0.67
11 Microhyla ornata											-	0.97	0.66
12 Microhyla heymonsi												-	0.62

Table 4. Spatial preference to land or stream for adults of the frogs and toads at the Wushikeng and Chichi stations (data, numbers of individuals observed)

Species	Wushikeng		Chichi	
	Land	Stream	Land	Stream
Bufo bankorensis *	156	332	1	51
Rhacophorus moltrechti *	67	9	140	6
Buergeria robustus *	1	108	0	81
Rana sauteri *	2	65	2	296
Rana latouchii *	110	25	172	423
Rana swinhoana *	32	118		
Polypedates megacephalus *			141	2
Chirixalus eiffingeri			24	43
Bufo melanosticus			27	26
Rana limnocharis			12	11
Rana guentheri			16	22
Microhyla ornata *			32	2
Microhyla heymonsi *			18	0

* Significant at 0.1% level (χ^2-test, p<0.001).

Table 5. The month of breeding climax of five species of frogs and toads commonly observed at the Wushikeng and Chichi stations

Species	Wushikeng	Chichi
Bufo bankorensis	February	December
Rhacophorus moltrechti	February	December
Buergeria robustus	August	August
Rana sauteri	December	October
Rana latouchii	February	December

above 500m in Taiwan. It was found at the Wushikeng Station all the year round, but was mainly observed in the cold months of the year at the Chichi Station. Its abundance was highest in December, constituting 82% of the total number of individuals observed in a year. At the Chichi Station, the climate may be too hot for its breeding activity except in winter. This species may migrate from high elevation to low elevation with the dropping of temperature in winter (Huang 1991).

Based on lengths of breeding durations, Wittenberger (1981) divides animals into two breeding types: explosive breeding and prolonged breeding. *B. bankorensis* at the Chichi Station (low elevation) could be categorized as a specialist with explosive breeding, whereas at the Wushikeng Station (high elevation) it was a generalist with prolonged breeding. In contrast to *B. bankorensis, R. sauteri* had the narrowest temporal niche breadth among the frogs at both stations (Table 1). It is an explosive breeder, and is known to have a short breeding period (Kuramoto *et al.* 1984; Lai *et al.* 2003). In the mountain region of Taiwan, *R. sauteri* may be divided into three populations according to their breeding seasons (Lai *et al.* 2003). The population at elevations of 240m to 1,000m found in this study belongs to the fall breeding population.

In this study the B_i-values of the species at the Wushikeng Station were generally higher than those of the same species at the Chichi Station (Table 1), suggesting that the temporal niche breadth of a species increased with the elevation up to 1,000m. There were 12 species at Chichi, but only 6 species at Wushikeng, suggesting that the species diversity of frogs decreased with the increase in elevation. Higher species diversity in the frog community at the Chichi Station, as compared to that of the Wushikeng Station, might be also a factor that reduced the niche breadth of the species (Table 1), but at the same time, increased niche overlap among species (Tables 2 and 3).

Amphibians show physiological and behavioral responses to fluctuations in surrounding environments, such as temperature (Brattstrom 1979; Hutchison and Dupre 1992), light illumination (Church 1961), and water availability (Dole and Durant 1974; Harris 1975; Pough *et al.* 1983; Cree 1989). Among these environmental factors, temperature has been considered to be the most important modulator for the amount of time available for activity of frogs (Tracy and Christian 1986). The monthly mean temperatures at Wushikeng were significantly lower than that at Chichi, but the monthly mean temperature curves at the two stations were similar (Fig. 2). The lower temperature at Wushikeng comparing to that at Chichi might be an important factor causing the lower species diversity, the wider temporal niche breadths (B_i) (Table 1), and wider temporal niche overlaps (α_{yx}) for the species (Tables 2 and 3). The only exception was *B. robustus* that had similar B_i-value between Wushikeng and Chichi station. Chu (1996) suggests that in the northern Taiwan, *B. robustus* has the same active season in spring and summer at elevations of 350m and 700m, similar to the case found for the species at elevations of 240m and 1,000m in this study.

Temporal niche overlap

Niche overlap value has been found to be a function of the relative abundance of frogs in the same niche dimension (Dash and Mahanta 1993). The lowest value of temporal niche overlap was found between *Rh. moltrechti* and *R. sauteri* at the Wushikeng station and between *R. sauteri* and *M. heymonsi* (or *M. ornata*) at the Chichi Station (Tables 2 and 3). The lowest value at each station suggested that the temporal niches might be an ecological character useful in niche differentiation between the two species. On the other hand, the highest value of temporal

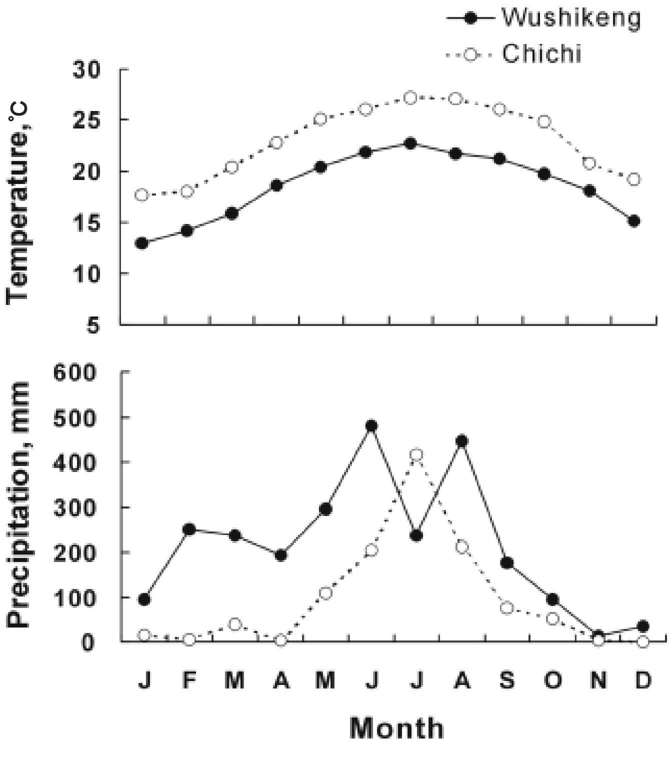

Fig. 2. Monthly average temperature and precipitation at the Wushikeng Station (1997-1998) and at the Chichi Station (2000 -2001).

niche overlaps was observed between *Rh. moltrechti* and *R. latouchii* at Wushikeng, and between *P. megacephalus* and *B. robustus* at Chichi (Tables 2 and 3). The highest value might suggest the presence of different niche dimension to reduce their competition in the frog community at each of the two stations. At Wushikeng *R. latouchii* was usually found to associate with the bottom substrates of still water bodies, whereas *Rh. moltrechti* was predominantly associated with aquatic vegetation. At Chichi *P. megacephalus* preferred land habitat, but *B. robustus* to the stream habitat (Table 4).

In this study *B. bankorensis* and *B. melanostictus* were found to have the widest temporal niche breadths (Table 1) with the highest values of average temporal niche overlaps (Tables 2 and 3) at Wushikeng and Chichi, respectively. The two species have wide ranges of tolerance to environmental gradients, so that they are easy to overlap with other species (Dash and Mahanta 1993).

Spatial preference

Based on the difference in abundance of adults at the land and stream substations (Table 4), *Rh. moltrechti, P. megacephalus, M. ornata* and *M. heymonsi* were considered as the frogs that preferred terrestrial habitats, whereas *B. bankorensis, B. robustus, R. sauteri,* and *R. swinhoana* preferred aquatic habitats. *C. eiffingeri, B. melanosticus, R. limnocharis* and *R. guentheri* did not show preference to either land or stream. Only *R. latouchii* that had different habitat preference between the two stations: stream preference at the Chichi Station and terrestrial preference at the Wushikeng Station. It seems that *R. latouchii* possess a strong flexibility in adaptation to the different habitats. We suspected that the difference in precipitation at different elevations affected water availability, and *R. latouchii* responded to the difference by changing its spatial preference. At the Wushikeng Station where precipitation was high and stream flow was faster all the year round, the frog tended to live in the land with still water bodies (Fig. 2). On the other hand, at the Chichi Station, where precipitation was low and the streams often dried up in fall or winter, the frog was only found in the streams with slow flowing water.

Breeding season

Beattie (1985) recorded the first spawning dates of *Rana temporaria* in a series of ponds over four years, and found that the initiating spawning of this species was delayed by six days for every 100m increase in altitude. Apparently, the timing of breeding is probably controlled not only by circannual endogenous rhythm but also by elevation. In this study, the elevation difference between the two stations was 850m. According to Beattie (1985), the frogs at the Wushikeng might delay their first spawning for 52 days. Although we did not record the time of first spawning, this phenomenon might indicate the lateness of breeding climax by two months at Wushikeng as compared to that at Chichi (Table 5).

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The Mindoro Snake Eel *Lamnostoma mindorum* (Jordan and Richardson) of the Hsiukuluan River in the Eastern Taiwan

台灣東部秀姑巒溪民多羅龍口蛇鰻

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Abstract

The Mindoro snake eel *Lamnostoma mindorum* (Jordan and Richardson, 1908) in the Hsiukuluan River of the eastern Taiwan occurred in the winter and early spring seasons of low water flow, and had two age classes at the modes of 34-37 cm and 46-49 cm in total length (juvenile and immature adult). These provided additional evidences to its rarity in freshwater near the mouth of rivers that the Mindoro snake eel is a peripheral freshwater fish defined as one that lives and spawns in ocean but some of its individuals occasionally intrude into freshwater streams.

摘要

台灣東部秀姑巒溪民多羅龍口蛇鰻(*Lamnostoma mindorum*)爲周緣性淡水魚，於冬天至春天低流量時偶然進入淡水河口，體長分兩群34-37 cm及46-49 cm，代表兩年齡群，在河內覓食底棲魚蝦。

Key words: *Lamnostoma mindorum*, ecology

關鍵詞：民多羅龍口蛇鰻、生態學

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The Mindoro snake eel *Lamnostoma mindorum* (Jordan and Richardson, 1908) is one of the rare species in the West Pacific. Up to date only five specimens have been reported from five localities: Baco River of Mindoro (Jordan and Richardson 1908; Herre 1923) and Abra River of Luzon (Herre 1953), Philippines; Waiho River, New Guinea (Weber and de Beaufort 1916); and Hsiukuluan River (Hatooka and Yoshino 1998) and Limpen River (Chang and Tsai 2003), Taiwan. Chen and Fang (2001) mentioned the occurrence of the Mindoro snake eel in the eastern Taiwan, but no mention was made on the number of individuals collected and the localities of their collections. Except its taxonomy and distribution, there was almost no biological information available for this species.

The Mindoro snake eel was collected primarily in freshwater, so that it has been speculated as a catadromous fish that lives in freshwater but spawns in ocean (Chen and Fang 2001). Because of its rarity and most of its collection sites near mouths of rivers, it has been also speculated as a peripheral freshwater fish defined as a species that lives and spawns in ocean but some of its individuals occasionally or accidentally intrude into the freshwater portion of rivers (Chang and Tsai 2003).

According to local fishermen, the Mindoro snake eel has often been caught in the lower Hsiukuluan River in the Hualien County. The collection site of the first record of this species to Taiwan by Hatooka and Yoshino (1998) was also in this river. It is one of the few rivers in Taiwan that retains a fairly natural condition. We conducted a bimonthly survey with electric fishing (150-200 volts, DC) from December 2002 to September 2003 in the area about 1.5 km from the mouth of the river and 0.5 km downstream from the Ch'ang-Hung Bridge of Rt. 11. As the river bed is higher than the sea level, the river water flows directly into sea without formation of the brackish water zone within the river. All Mindoro snake eels were collected in the freshwater zone with water conductivity between 388 μs/cm and 443 μs/cm (equivalent to salinity about 0.2 ppt).

A total of nine Mindoro snake eels were collected in the winter and spring months from December to April at water temperature of 21.5℃ to 23.5℃. No eel was found in the summer months from July to September at 28.4℃ and 29.6℃. Of them seven eels were collected in April (Table 1). In the Hsiukuluan River, the Mindoro snake eel occurred in correspondence with the season of low water flow (Fig. 1). In other words, the occurrence of the Mindoro snake eels in the Hsiukuluan River was not all the year round but seasonal.

The nine Mindoro snake eels collected ranged between 31 cm and 53.5 cm, and consisted of two size classes at the modes of 34-37 cm and 46-49 cm in the length frequency distribution (Fig. 2). These two size classes indicated the presence of two age classes of Mindoro snake eels in the river. When the lengths of a specimen reported from the Hsiukuluan River by Hatooka and Yoshino (1998) and of three specimens from other rivers in the West Pacific (Jordan and Richardson 1908; Weber and de Beaufort 1916; Herre 1923) were also added in the length frequency distribution (Fig. 2), the two size classes became more distinctive. Apparently, the size composition of the Mindoro snake eels in the Hsiukuluan River may also occur in other rivers.

Table 1. Number of Mindoro snake eels collected, and their total length and weight (mean; ranges in parentheses) from the Hsiukuluan River, eastern Taiwan, and concurrent water temperature, water conductivity

Date	Water temperature (℃)	Conductivity (μs/cm)	Specimen		
			Number	Total length (cm)	Weight (g)
5 Dec. 2002	22.8	389	1	53.5	134
13 Feb. 2003	21.5	412	1	47.0	77
1 Apr. 2003	23.5	443	7	42.8 (31-48)	72.5 (30-106)
8 Jul. 2003	28.4	400	0	-	-
30 Sep. 2003	29.6	388	0	-	-

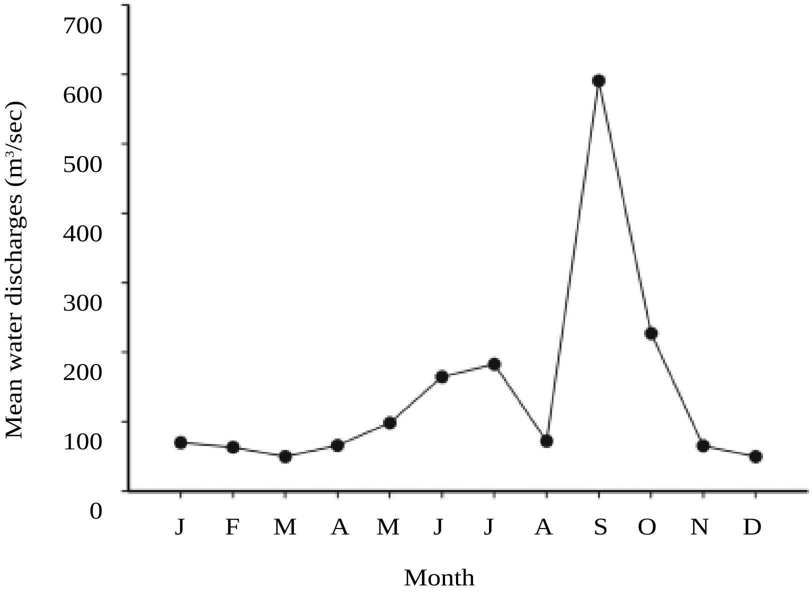

Fig. 1. Monthly mean water discharges (m^3/sec) of the Hsiukuluan River measured at the Juisui Bridge, 2001 (data obtained from the Water Resources Agency of the Ministry of Economics, Taiwan).

Although their exact ages were unknown, based on their sizes they were estimated to be 2- or 3-year old juveniles and 3- or 4-year old immature adults. There were no specimens of the young year class with total length shorter than 31 cm. Because the samples collected were still too small, a further collection was required for the age composition confirmation.

We dissected the 53.5 cm specimen collected from the Hsiukuluan River and the

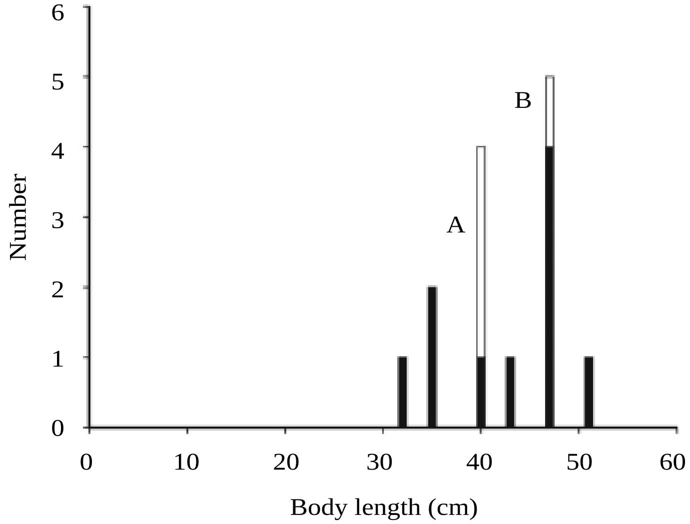

Fig. 2. A frequency distribution of total lengths of *Lamnostoma mindorum* collected from the Hsiukuluan River (solid columns) and other rivers [open column A, one specimen each from Jordan and Richardson (1908), Weber and de Beaufort (1916), and Herre (1923); open column B, one specimen from Hatooka and Yoshino (1998)].

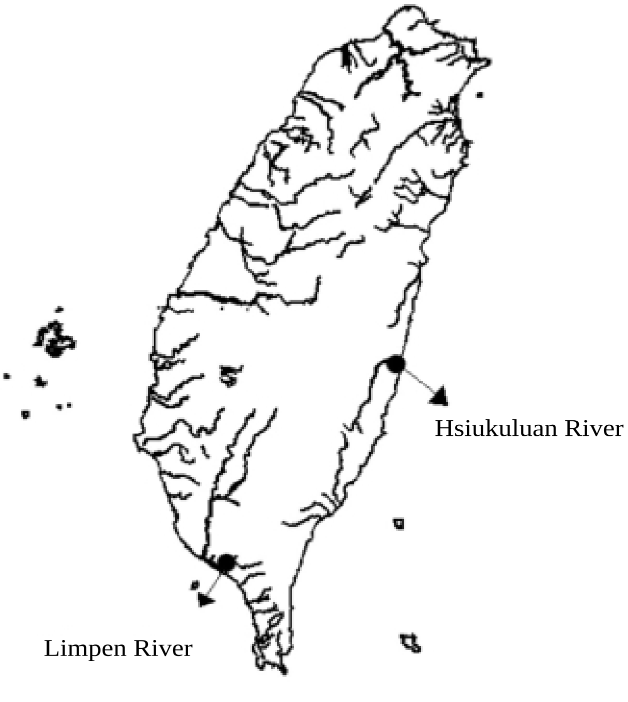

Fig. 3. Distribution of *Lamnostoma mindorum* (solid circles) in Taiwan.

40 cm specimen collected from the Limpen River (Chang and Tsai 2003) (Fig. 3). The gonads were small and string like. They were either at the immature or the resting stage of reproduction. The stomach contents were also examined. The large specimen had a partially digested goby (6.7 cm, 2.5g), and the small one had a well preserved shrimp (*Macrobranchium* sp., 5.63 cm, 2.9g). The tails of both preys in the stomachs pointed toward the eels’ anus, suggesting that they were swallowed by the eels with their tails first.

Although the data collected in this study was limited, the Mindoro snake eels collected from the Hsiukuluan River showed a seasonal occurrence with two age classes of juveniles and immature adults. If we adopt the notion that the Mindoro snake eel is a catadromous fish as Chen and Fang (2001) speculated, we should have been able to find not only the two age classes (juvenile and immature adult) but also other younger classes all the year round. The seasonal occurrence of only two age classes in the Hsiukuluan River provided additional evidence for the alternative notion that the Mindoro snake eel was a peripheral freshwater fish and those individuals collected in the freshwater rivers were occasional intruders from the ocean (Chang and Tsai 2003). As the samples collected were still too small, further studies are required for confirmation of this notion.

We kept a Mindoro eel (47 cm) collected on 1 April 2003 from the Hsiukuluan River in aquarium for observation. The eel buried in sand bottom with its head or only its snout portion above the bottom surface in day time, and lay on the bottom surface in night. In the Hsiukuluan River, all specimens of the Mindoro snake eel was collected from sand and clay bottom with an electric shocker. This bottom doweling habit and habitat may be one of the reasons for its rarity to be found in fresh water, and also the reason that it has never been found in the sea.

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利用掃瞄式電子顯微鏡(SEM)技術觀察台灣產10種碗蕨科孢子形態

A Morphological Study on Spores of 10 Species of Dennstaedtiaceae from Taiwan with Scanning Electron Microscopy Technique

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摘　要

本研究乃利用掃描式電子顯微鏡(SEM)觀察採自台灣各地碗蕨科5屬10種孢子的細微構造，經觀察結果綜合比較發現，孢子細微構造的特徵，可作爲碗蕨科5個屬間及所包括的10個物種間鑑定上輔助的依據。姬蕨屬及栗蕨屬等2屬的孢子爲單裂縫型，其中栗蕨屬的孢子不具周壁，姬蕨屬的孢子具周壁且呈刺狀紋飾而可與前一屬區分。稀子蕨屬、碗蕨屬及鱗蓋蕨屬等3屬的孢子爲三裂縫型，其中稀子蕨屬的孢子外壁不具明顯紋飾可與外壁具紋飾的碗蕨屬及鱗蓋蕨屬區分；而碗蕨屬孢子外壁呈明顯的細網狀紋飾可與孢子外壁呈不同程度加厚或呈顆粒狀紋飾的鱗蓋蕨屬區分。孢子微細構造除了作爲碗蕨科屬間的分類依據外並可進一步作爲種間的分類特徵，姬蕨屬中姬蕨的孢子具裂縫且一端呈兩分叉狀，細葉姬蕨的孢子不具明顯裂縫而可區分開。碗蕨屬中碗蕨的孢子外壁表面形成不同程度加厚的帶狀紋飾，與具顆粒狀紋飾的細毛碗蕨的孢子可容易的區別。鱗蓋蕨屬中的虎克氏、熱帶、粗毛及亞粗毛鱗蓋蕨，則可藉由孢子周壁的增厚情形及紋飾的不同而加以區別。

Abstract

Spores of 10 species in five genera of the family Dennstaedtiaceae were examined, using the scanning electronic microscopy (SEM) technique. The fine structure of the spores was found to be a useful diagnostic character for the generic and specific distinction for Dennstaedtiaceae. Spores of the genera *Hypolepis* and *Histiopteris* are monolete and the two genera are distinguishable by difference in their perispore grains types, while those of the genera *Monachosorum*, *Dennstaedtia*, and *Microlepia* are trilete, and the three genera are distinguishable by their exine grain types. For distinction of congeneric species, fissure margos of spores is a useful character for distinguishing two species of *Hypolepis: H. punctata* (Thunb.) Mett. and *H. tenuifolia* (Forst.) Bernh., the exine grains for two species of *Dennstaedtia: D. scabra* (Wall.) Moore and *D. hirsuta* (Sw.) Mett. *ex* Miq., and thickness and grains for four species of *Microlepia: M. hookeriana* (Wall.) Presl, *M. speluncae* (L.) Moore, *M. strigosa* (Thunb.) Presl, and *M. substrigosa* Tagawa.

關鍵詞：孢子、掃瞄式電子顯微鏡、碗蕨科

Key words: spore, scanning electron microscopy, Dennstaedtiaceae

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緒　言

台灣由於地形的特殊性，造就了生態系統的多樣性，在全世界約12,000種蕨類植物中，台灣就包含了約600多種的蕨類植物，和世界上其他地區相較，台灣可說是全世界蕨類植物物種密度最高的地區(郭 1999)。台灣地區植物的研究從日據時代開始就從未間斷，其中關於蕨類植物的研究也極爲詳細，但由於採用的分類方法略有差異，造成蕨類植物分類上的差異，根據台灣維管束植物科誌(黃 1993)及台灣植物圖鑑(鄭 2000)書中採用的分類系統，共將台灣蕨類分爲37科；但台灣維管束植物科簡誌第一卷(郭 1997)中採用Tryon及Kramer的分類系統，則只將蕨類分爲33科，本篇研究採用Flora of Taiwan (Editorial Committee of the Flora of Taiwan, 1993-2003)的分類系統，將碗蕨科植物分爲7屬27種(包含兩變種)。

以往我國學者曾根據蕨類植物之孢子囊群、毛、鱗片等肉眼可辨識的特徵，進行分類學研究(蔡 1978)，並據以建立台灣原生蕨類植物之檢索表。雖已有檢索表可供物種辨識，但仍有些種類因其差異太小致難以辨

識。近年來，電子顯微鏡被運用於觀察蕨類孢子的形態及紋飾構造，對於古生代之維管束植物孢子及花粉之基本構造，有明確的特定特點可區別植物種間之類緣關係，並可推演其發源地理分布(Taylor 1973)。掃描式電子顯微鏡(SEM)具有極高度的放大、解析功能，爲觀察生物材料微細構造極佳工具，可清楚地觀察蕨類植物之孢子形態及紋飾特徵(張等 1974；Devi 1975)。因此，國外學者利用掃描式電顯技術，從事此一方面的研究，且已有部分屬、種因新資料的獲得而被重置分類地位(Haufler and Gastony 1978；Liew 1977；Montgomery and Taylor 1994；Moy 1988；Rasbach *et al*. 1994)。

在中國蕨類植物孢子形態(中國科學院北京植物研究所 1976)書中，中國碗蕨科植物以孢子形態特質作爲物種辨識及分類的依據，包括孢子大小、極面觀及赤道面觀之孢子形狀、孢子裂縫數、周壁有無、周壁厚度及外壁紋飾等，其中外壁的紋飾特徵被認爲是可靠的分類依據(Moy 1988)。在台灣由於少有利用電子顯微鏡(SEM)來觀察蕨類孢子的特徵，作爲蕨類植物中物種間或變種間的分類依據，至目前爲止只有數篇關於此方面的研究(文 1993a, 1993b；陳 1997；Liu *et al*. 2000)等研究。然而台灣蕨類植物中尙存在著一些很難利用常見的外部形質來分類的物種，所以，本研究乃利用電子顯微鏡技術來進行台灣產碗蕨科植物中10個種類孢子細微構造的觀察，並利用觀察的結果輔助碗蕨科各屬間及種間區別的依據

材料與方法

實驗材料部分採自中部地區，部分收集自農委會特有生物研究保育中心植物標本館館藏之標本；另外，栗蕨屬的栗蕨標本由中興大學劉思謙老師提供，本研究共收集了碗蕨科植物10種，分屬於5個屬。

本研究採樣前先以氣體將植物體表面清除雜物，再採取未裂開的孢子囊，將其於顯微鏡下操作切開、黏附在標本座上，放入眞空噴射鍍膜儀(Hitachi Ion Sputter E-1010)做鍍金處理，鍍金厚度約20 nm。鍍金後，置於掃描式電子顯微鏡(Hitachi 2460N)下，以電壓20 kV作孢子形態的觀察，並將觀測的孢子顯微構造，利用電腦程式將其影像存檔。記錄碗蕨科各屬間及各種間孢子的形質特徵，並比較其差異。

觀察結果

本研究總共觀察了碗蕨科中5屬10種孢子形態特徵，其掃描式電子顯微鏡下特徵分別描述如下。另外，曲軸蕨屬台灣只1屬1種，屬稀有蕨類植物，且只在台東有一次採集紀錄，本研究並未收集到。

姬蕨屬 *Hypolepis* Benth.

本屬孢子極面觀爲橢圓形，赤道面觀爲圓形、半圓形或豆形。孢子極軸長爲17.1-33.8 μm，赤道軸長爲34.0-43.9 μm。單裂縫，裂縫長度爲孢子全長的2/3或接近孢子赤道線，有些種類裂縫不明顯。周壁表面具不整齊的刺狀紋飾，有的成短棒狀，紋飾之間常有一層很模糊的薄膜圍繞著，刺長度爲1.5-7.1 μm，刺常不規則，或尖或鈍以及其他形狀。外壁表面呈現玦狀紋飾或模糊的網狀紋飾。

姬蕨*Hypolepis punctata* (Thunb.) Mett.

Fig. 1

姬蕨孢子極面觀爲橢圓形，赤道面觀爲豆形。孢子極軸長爲17.1-22.0 μm，赤道軸長爲34.0-40.5 μm。單裂縫，裂縫長度爲孢子全長的2/3以上，接近孢子赤道線，且裂縫的一

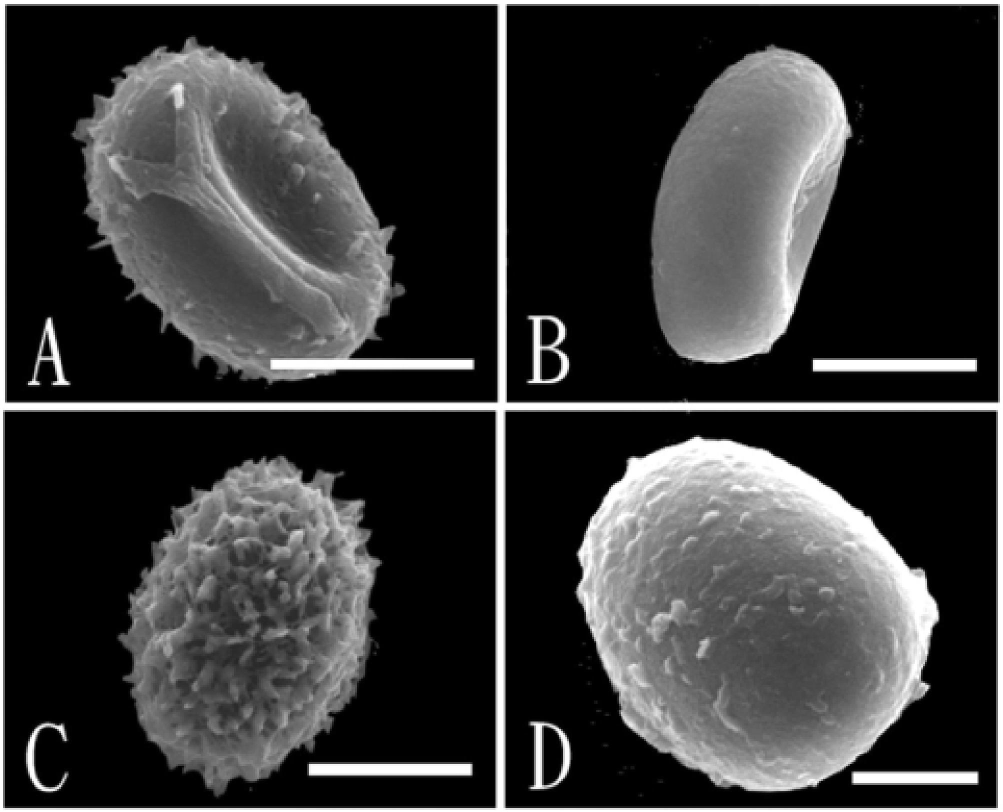

圖1. 姬蕨(*Hypolepis punctata*)孢子(A.近極面觀，Scale bar= 20 μm；B.赤道面觀，Scale bar=20 μm；C.遠極面觀，Scale bar= 20 μm；D.遠極面觀，Scale bar= 10 μm)。

Fig. 1. *Hypolepis punctata* spore (A. Proximal pole view; B. Equatorial view; C. Distal pole view; D. Distal pole view).

端成兩分叉狀。孢子具有兩型，有具有周壁者，也有不具周壁而直接呈現外壁紋飾者。具周壁孢子，周壁表面有不整齊的刺狀紋飾，紋飾之間常有一層很模糊的薄膜圍繞著，刺長度爲1.5-3.0 μm，刺常不規則，或尖或鈍以及其他形狀。不具周壁的孢子，顯現出外壁的块狀紋飾。

觀察標本：南投蓮華池，郭89001(國立彰化師範大學生物學系標本室)。

細葉姬蕨*Hypolepis tenuifolia* (Forst.) Bernh.

Fig. 2

細葉姬蕨孢子極面觀爲橢圓形，赤道面觀爲圓形或半圓形。孢子極軸長爲26.3-33.8 μm，赤道軸長爲35.9-43.9 μm。單裂縫，裂縫不明顯。周壁表面具不整齊的刺狀紋飾，刺長度爲3.15-7.1 μm，刺常不規則，或尖或鈍以及其他形狀。周壁的刺狀紋飾較長於姬蕨。少部分孢子不具周壁而呈現外壁模糊的網狀紋飾。

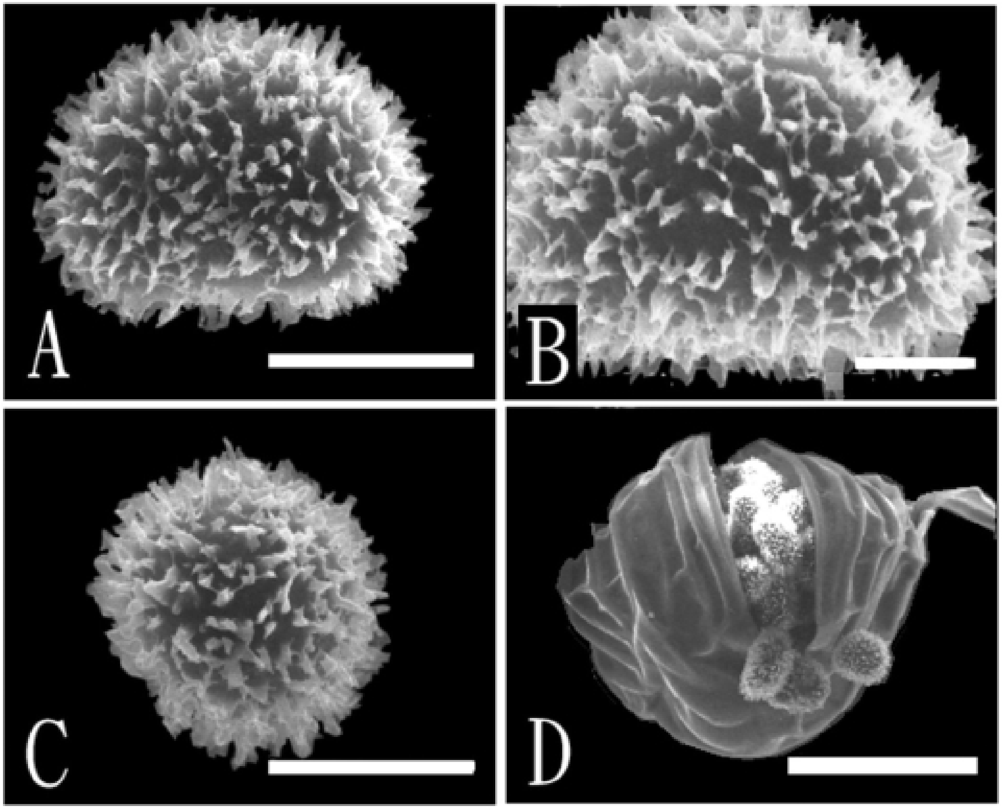

圖2. 細葉姬蕨(*Hypolepis tenuifolia*)孢子(A.極面觀，Scale bar= 20 μm；B.極面紋飾，Scale bar=10 μm； C.赤道面觀，Scale bar= 20 μm； D.孢子與孢子囊，Scale bar= 100 μm)。

Fig. 2. *Hypolepis tenuifolia* spore (A. Polar view; B. Polar view with exine sculpture; C. Equatorial view ; D. Spore and sporangium).

觀察標本：雲林古坑，陳1469(特有生物研究保育中心標本館)。

栗蕨屬*Histiopteris* (Ag.) J. Sm.

本屬孢子爲單裂縫型，呈左右對稱，極面觀爲橢圓形或寬橢圓形，赤道面觀爲半圓形或超半圓形。孢子極軸長爲20.2-24.5μm，赤道軸長爲31.2-34.4μm。具單裂縫，裂縫不具邊緣，裂縫長度爲孢子全長的2/3或接近孢子赤道線。外壁表面具疣块狀紋飾，疣块較矮，形狀不規則，大小不一致，基部連接，在疣块之間尚具小穴構造。

栗蕨*Histiopteris incisa* (Thunb.) J. Sm.

Fig. 3

孢子具單裂縫，呈左右對稱，極面觀爲橢圓形或寬橢圓形，赤道面觀爲半圓形或超半圓形。孢子極軸長爲20.2-24.5 μm，赤道軸長爲31.2-34.4μm。裂縫不具邊緣，裂縫長度爲孢子全長的2/3或接近孢子赤道線。外壁表

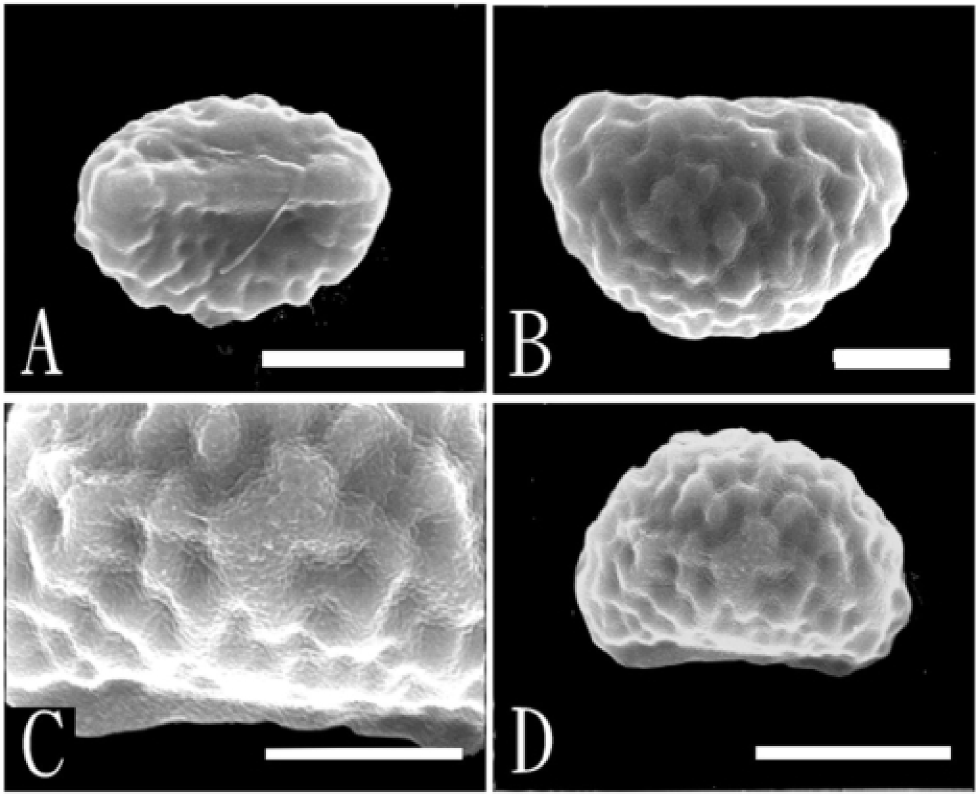

圖3. 栗蕨(*Histiopteris incisa*)孢子(A.近極面觀，Scale bar= 20 μm； B.遠極面觀，Scale bar= 10 μm； C.外壁不規則疣玦狀紋飾，Scale bar= 10 μm； D.赤道面觀，Scale bar= 20 μm)。

Fig. 3. *Histiopteris incisa* spore (A. Proximal pole view; B. Distal pole view; C. Irregular verrucate perispore; D. Equatorial view).

面具疣玦狀紋飾，疣玦較矮，形狀不規則，大小不一致，基部連接，在疣玦之間尚具小穴構造。

觀察標本：南投日月潭，劉851229(中興大學生命科學系標本館)。

碗蕨屬*Dennstaedtia* Bernh.

本屬孢子極面觀爲鈍三角形，赤道面觀爲半圓形或寬橢圓形。孢子極軸長爲21.3-35.3μm，赤道軸長爲24.6-49.0μm。三裂縫，裂縫長度爲孢子赤道半徑的1/2-2/3或接近孢子赤道線。具周壁或不具周壁，外壁紋飾有以下兩種情況：1.外壁表面形成各種不同程度的加厚，一般在近極面比較均匀，形成三角形，在赤道面和遠極面則較不均匀，形成不規則的疣狀、帶狀或細網狀紋飾。2.外壁具明顯的顆粒狀紋飾。

碗蕨*Dennstaedtia scabra* (Wall.) Moore

Fig. 4

孢子極面觀爲鈍三角形，赤道面觀爲寬橢圓形。孢子極軸長爲21.3-25.2μm，赤道軸

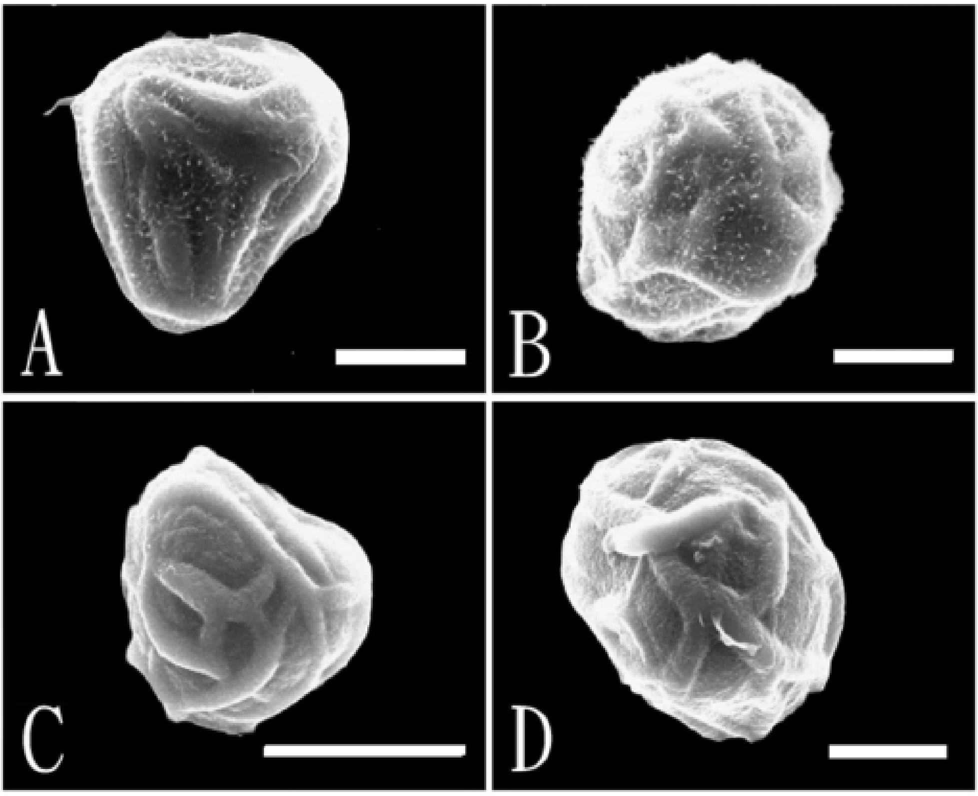

圖4. 碗蕨(*Dennstaedtia scabra*)孢子(A.近極面觀，Scale bar= 10 μm； B.赤道面觀，Scale bar= 10 μm； C.遠極面觀，Scale bar= 20 μm； D.赤道面觀，Scale bar= 10 μm)。

Fig. 4. *Dennstaedtia scabra* spore (A. Proximal pole view; B. Equatorial view; C. Distal pole view; D. Equatorial view).

長爲24.6-29.1μm。三裂縫，裂縫長度爲孢子赤道半徑的2/3或接近孢子赤道線。外壁表面形成不同程度的加厚，在近極面加厚較均勻，沿著裂縫形成很明顯的三角形加厚，在赤道面和遠極面加厚形成帶狀紋飾。少部分孢子在增厚的外壁上具有毛狀構造。

觀察標本：台中東卯山，黃1182(特有生物研究保育中心標本館)。

細毛碗蕨*Dennstaedtia hirsuta* (Sw.) Mett. *ex* Miq.

Fig. 5

孢子極面觀爲鈍三角形，赤道面觀爲半圓形。孢子極軸長爲23.6-35.3μm，赤道軸長爲33-49μm。三裂縫，裂縫長度爲孢子赤道半徑的1/2-2/3，不具邊緣。孢子不具周壁。外壁常形成不規則的顆粒狀紋飾。

觀察標本：嘉義豐山，陳2440(特有生物研究保育中心標本館)。

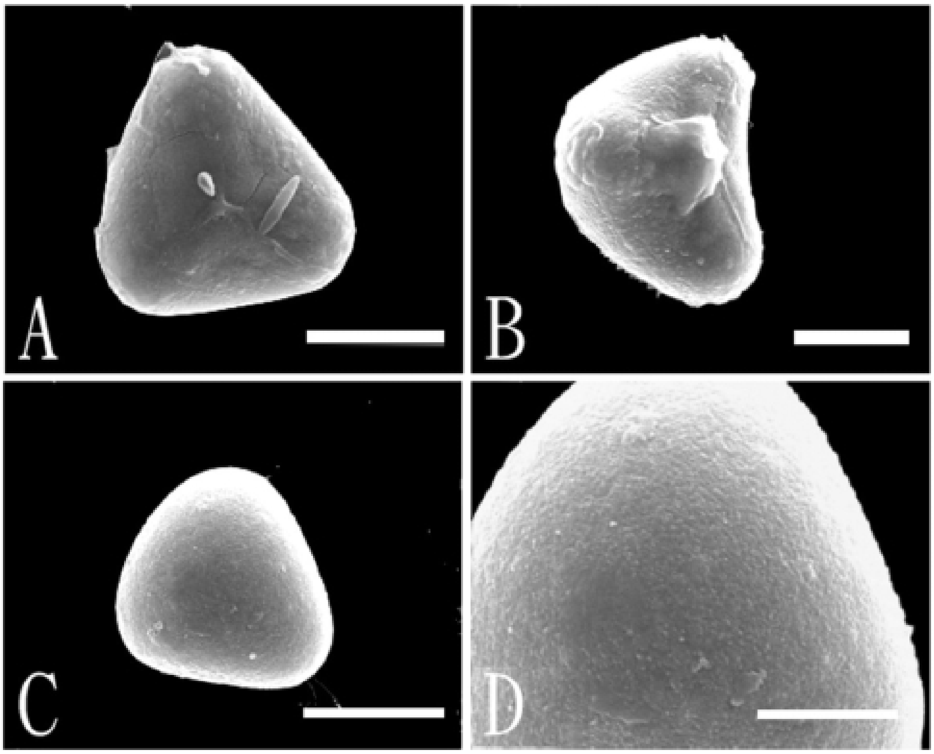

圖5. 細毛碗蕨(*Dennstaedtia hirsuta*)孢子(A.近極面觀，Scale bar= 20 μm； B.赤道面觀，Scale bar= 20 μm； C.遠極面觀，Scale bar= 20 μm； D.顆粒狀紋飾，Scale bar= 10 μm)。

Fig. 5. *Dennstaedtia hirsuta* spore (A. Proximal pole view; B. Equatorial view; C. Distal pole view; D. Granuliferous perispore).

鱗蓋蕨屬*Microlepia* Presl

本屬孢子極面觀爲鈍三角形，三腰稍凹入，赤道面觀爲寬橢圓形或橢圓形，少數爲半圓形。孢子極軸長爲21.6-37.0μm，赤道軸長爲33.3-41.8μm。三裂縫，裂縫長度爲孢子赤道半徑的1/2-2/3或接近孢子赤道線。在本屬不少種類的孢子中，裂縫既有開裂的，也有不開裂的，開裂者具有明顯的邊緣，不開裂者不具邊緣。孢子具周壁或不具周壁，在某些種類中不能確定。周壁具模糊的網狀紋飾，棒狀紋飾或瘤狀突起紋飾。外壁具明顯的細網狀紋飾，爲本屬孢子共有的外壁紋飾特徵。

虎克氏鱗蓋蕨*Microlepia hookeriana* (Wall.) Presl

Fig. 6

孢子極面觀爲鈍三角形，赤道面觀爲寬橢圓形。孢子極軸長爲25.1-37μm，赤道軸長爲35.1-41.8μm。三裂縫，裂縫長度爲孢子赤道半徑的2/3或接近孢子赤道線，裂縫邊緣具周壁增厚的現象，周壁具模糊的網狀紋飾；少數孢子不具周壁，而顯現出細網狀的外壁紋飾。

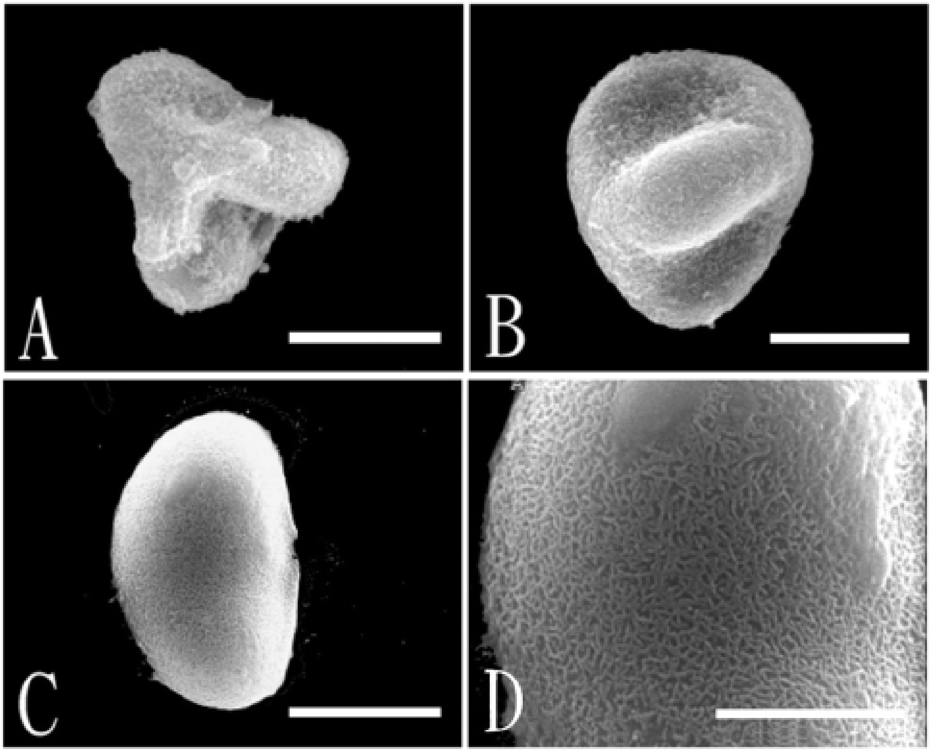

圖6. 虎克氏鱗蓋蕨(*Microlepia hookeriana*)孢子(A.近極面觀，Scale bar=20 μm； B.赤道面觀，Scale bar= 20 μm； C.遠極面觀，Scale bar= 20 μm； D.細網狀外壁紋飾，Scale bar= 10 μm)。

Fig. 6. *Microlepia hookeriana* spore (A. Proximal pole view; B. Equatorial view; C. Distal pole view; D. Fie reticulate perispore).

觀察標本：南投蓮華池，郭89002(特有生物研究保育中心標本館)。

熱帶鱗蓋蕨 *Microlepia speluncae* (L.) Moore

Fig. 7

孢子極面觀爲鈍三角形，赤道面觀爲橢圓形。孢子極軸長爲21.6-27μm，赤道軸長爲37.3-40.5μm。三裂縫，裂縫長度爲孢子赤道半徑的2/3，具邊緣。外壁具明顯的細網狀紋飾，且有少部分的毛狀突起。

觀察標本：雲林斗六，陳1260(特有生物研究保育中心標本館)。

粗毛鱗蓋蕨*Microlepia strigosa* (Thunb.) Presl

Fig. 8

孢子極面觀爲鈍三角形，赤道面觀爲橢圓形。孢子極軸長爲21.6-31.7μm，赤道軸長爲34.7-40.0μm。三裂縫，裂縫長度爲孢子赤道半徑的1/2，不具邊緣，或裂縫不明顯。孢子具兩型，多數孢子不具周壁而呈現外壁的細網狀紋飾，並偶有周壁的殘留形成毛狀突起，少數孢子具周壁，呈現明顯的瘤狀突起紋飾。

觀察標本：南投紅香，文205(特有生物

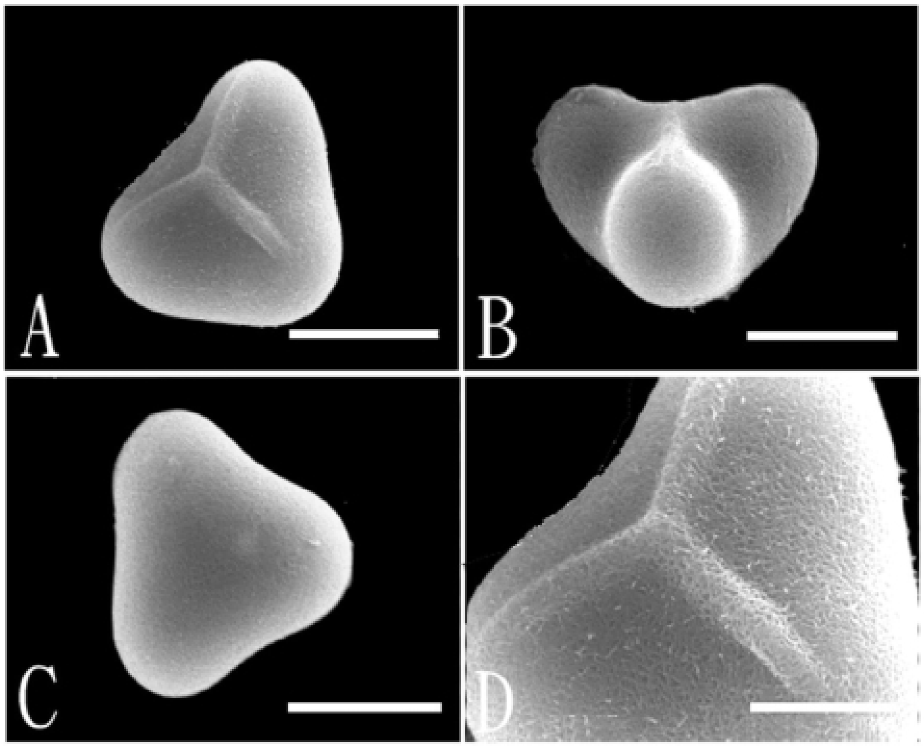

圖7. 熱帶鱗蓋蕨(*Microlepia speluncae*)孢子(A.近極面觀，Scale bar= 20 μm； B. 赤道面觀，Scale bar= 20 μm； C.遠極面觀，Scale bar= 20 μm； D.細網狀外壁紋飾，Scale bar= 10 μm)。

Fig. 7. *Microlepia speluncae* spore (A. Proximal pole view; B. Equatorial view; C. Distal pole view; D. Fine reticulate perispore).

研究保育中心標本館)。

亞粗毛鱗蓋蕨 *Microlepia substrigosa* Tagawa

Fig. 9

孢子極面觀爲鈍三角形，赤道面觀爲橢圓形。孢子極軸長爲28-35.1μm，赤道軸長爲33.3-40.3μm。三裂縫，裂縫長度爲孢子赤道半徑的2/3，不具邊緣。孢子具兩型，多數孢子具周壁且具明顯的棒狀突起，少數孢子無周壁，外壁呈現明顯的細網狀紋飾。

觀察標本：雲林古坑，陳1512(特有生物研究保育中心標本館)。

稀子蕨屬 *Monachosorum* Kunze

本屬孢子具三裂縫，極面觀爲鈍三角形，三邊略內凹，赤道面觀爲半圓形。孢子極軸長度爲15.2-18.3μm，赤道軸長度爲30.1-34.8μm。孢子裂縫長度爲孢子半徑的1/2-2/3。不具周壁。外壁表面具不明顯的疣狀和稀少的瘤狀紋飾，瘤分布不均勻；或外壁表面有時具有不規則的片狀紋飾。

稀子蕨 *Monachosorum henryi* Chist

Fig. 10

孢子極面觀爲鈍三角形，三邊略內凹，赤道面觀爲半圓形。孢子極軸長度爲15.2-

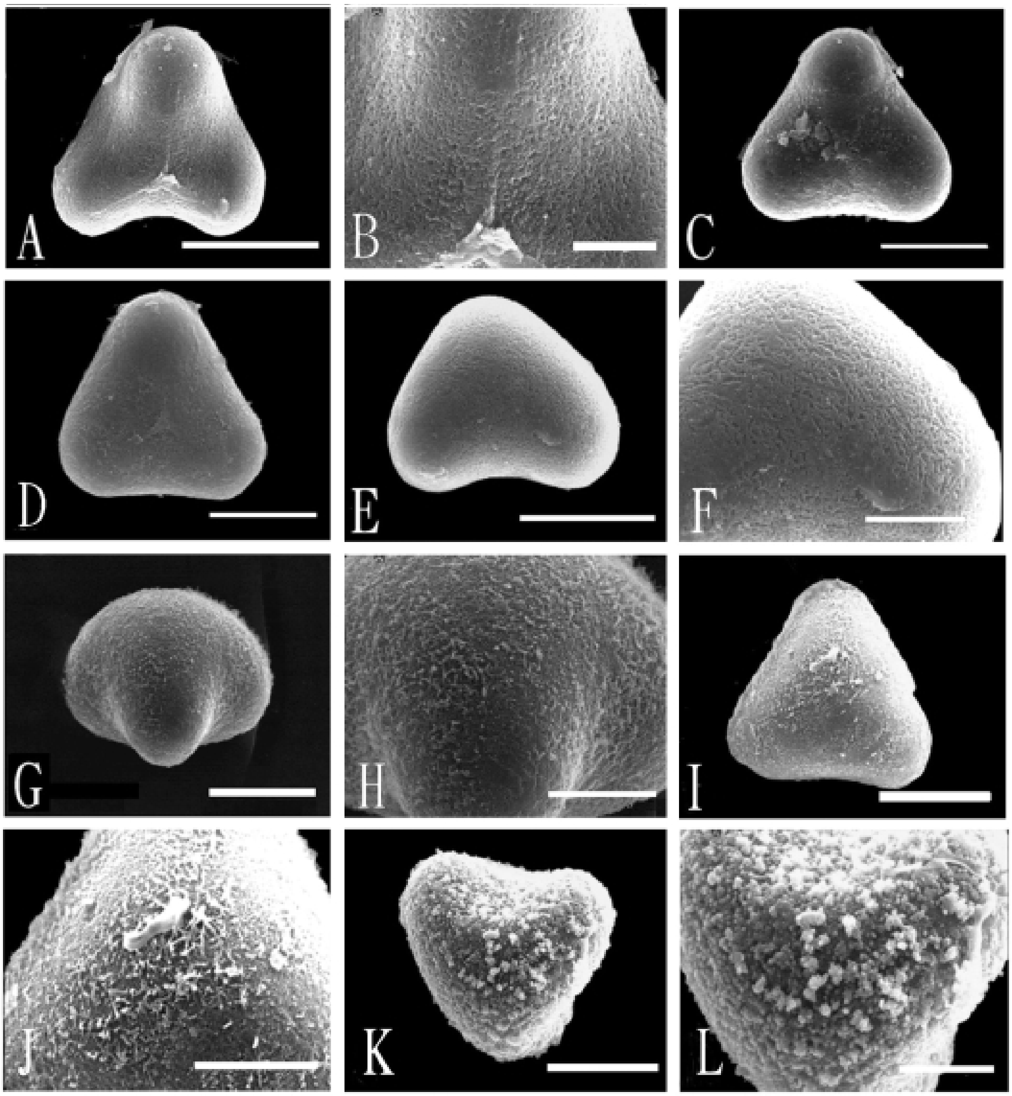

圖8. 粗毛鱗蓋蕨(*Microlepia strigosa*)孢子(A.近極面觀，Scale bar= 20 μm； B. 外壁細網狀紋飾，Scale bar= 5 μm； C.近極面觀(裂縫不明顯)，Scale bar=20 μm； D.近極面觀(裂縫不明顯)，Scale bar= 20 μm；E.遠極面觀，Scale bar= 20 μm； F.遠極面細網狀外壁紋飾，Scale bar= 20 μm；G.赤道面觀，Scale bar= 10 μm； H.赤道面細網狀外壁紋飾，且周壁殘留形成毛狀突起，Scale bar= 20 μm； I.遠極面觀，Scale bar= 20 μm； J.遠極面觀細網狀外壁紋飾，且周壁殘留形成毛狀突起，Scale bar= 10 μm； K.遠極面觀，Scale bar= 20 μm； L.周壁瘤狀突起紋飾，Scale bar= 10 μm)。

Fig. 8. *Microlepia strigosa* spore (A. Proximal pole view; B. Fine reticulate perispore; C. Proximal pole view; D. Proximal pole view; E. Distal pole view; F. Distal pole with fine reticulate exine; G. Equatorial view; H. Equatorial view with fine reticulate exine, and trichomatic exine formed from residual perispore; I. Distal pole view; J. Distal pole with fine reticulate exine, and trichomatic exine formed from residual perispore; K. Distal pole view; L. Tuberculate perispore).

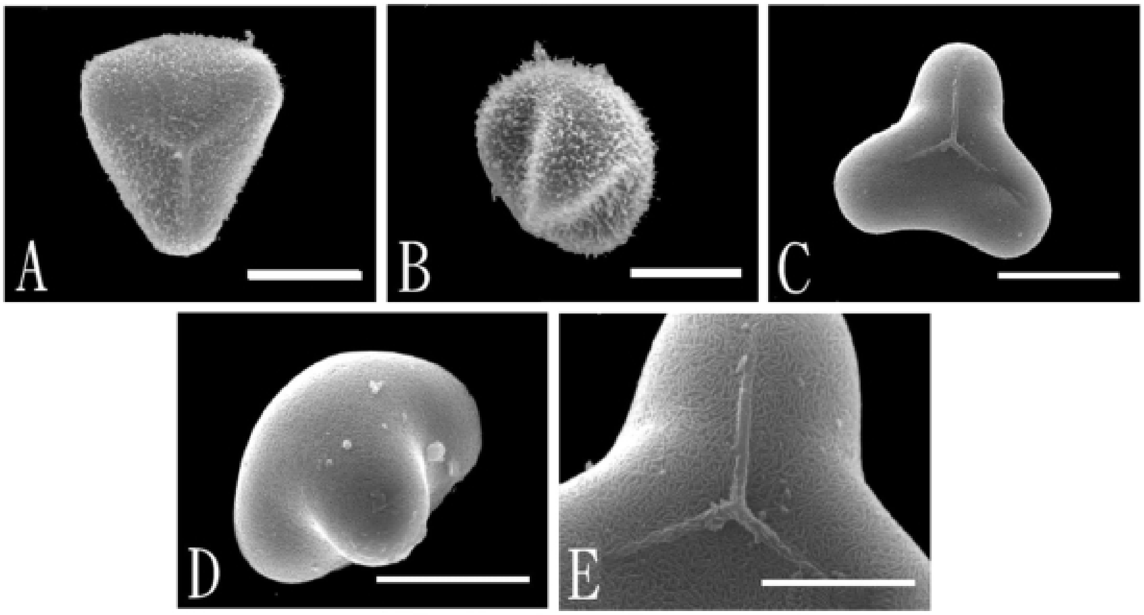

圖9. 亞粗毛鱗蓋蕨(*Microlepia substrigosa*)孢子(A.近極面觀，Scale bar= 20 μm； B. 赤道面觀，Scale bar= 20 μm； C.近極面觀，Scale bar= 20 μm； D.赤道面觀，Scale bar= 20 μm； E.近極面細網狀外壁紋飾，Scale bar= 10 μm)。

Fig. 9. *Microlepia substrigosa* spore (A. Proximal pole view; B. Equatorial view; C. Proximal pole view ; D. Equatorial view; E. Proximal pole with fine reticulate exine).

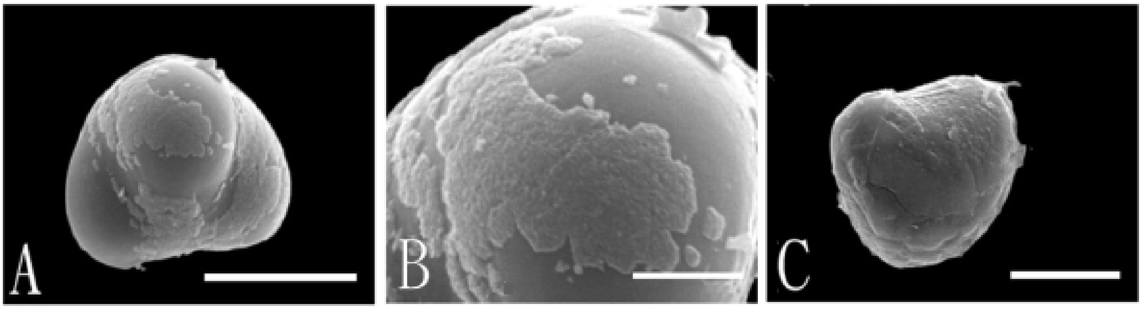

圖10. 稀子蕨(*Monachosorum henryi*)孢子(A.赤道面觀，Scale bar= 20 μm； B.外壁不規則的片狀紋飾，Scale bar= 5 μm； C.極面觀Scale bar= 20 μm)。

Fig. 10. *Monachosorum henryi* spore (A. Equatorial view; B. Irregular lamellate perispore; C. Polar view).

18.3 μm，赤道軸長度爲30.1-34.8 μm。具三裂縫，裂縫長度爲孢子半徑的1/2-2/3。不具周壁。外壁表面具不明顯的疣狀和稀少的瘤狀紋飾，瘤分布不均匀；或外壁表面有時具有不規則的片狀紋飾。

觀察標本：南投蓮華池，郭89003(特有生物研究保育中心標本館)。

本研究綜合掃瞄式電子顯微鏡所觀察碗蕨科10種蕨類孢子形態特徵，整理碗蕨科檢索表如下所示：

1.孢子爲單裂縫型..2
1.孢子爲三裂縫型..4
2.孢子外壁表面爲刺狀紋飾、块狀或網狀紋飾且孢子具或不具周壁.........姬蕨屬..........3
2.孢子外壁表面具疣块狀紋飾且孢子不具周壁..栗蕨(屬)
3.孢子裂縫一端成兩分叉狀......................姬蕨
3.孢子不具明顯裂縫..........................細葉姬蕨
4.孢子外壁具不明顯的疣狀及瘤狀紋飾且孢子不具周壁...................................稀子蕨(屬)
4.孢子外壁具明顯紋飾且孢子具周壁或不具周壁..5
5.孢子外壁呈顆粒狀紋飾或具不同程度加厚，形成不規則的疣狀、帶狀或細網狀紋飾...碗蕨屬.........6
5.孢子外壁呈細網狀紋飾.......鱗蓋蕨屬..........7
6.外壁表面形成不同程度的加厚而形成帶狀紋飾..碗蕨
6.外壁形成不規則的顆粒狀紋飾......細毛碗蕨
7.孢子裂縫具邊緣..8
7.孢子裂縫不具邊緣.......................................9
8.孢子邊緣具周壁增厚的現象...虎克氏鱗蓋蕨
8.孢子邊緣不具周壁增厚現象.......熱帶鱗蓋蕨
9.孢子不具周壁，外壁呈現明顯的瘤狀突起紋飾...粗毛鱗蓋蕨
9.孢子具周壁，外壁呈明顯的棒狀突起紋飾...亞粗毛鱗蓋蕨

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Ambrosia psilostachya DC. (Asteraceae) a Newly Naturalized Plant in Taiwan

台灣新歸化菊科（Asteraceae）裸穗豬草

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Abstract

This paper describes *Ambrosia psilostachya* DC. (Asteraceae) as a plant newly recorded to Taiwan. It has established its feral population in Kaohsiung County, and is closely related to exotic *A. artemisiaefolia* L. of Taiwan. However, the two species are distinguishable by the structure of their pinnatifid leaves. This paper also provides its distribution, living habitat, breeding (flowering and fruiting) period.

摘要

裸穗豬草(菊科)首次在高雄市左營區半屏山頂被採集，爲台灣新歸化植物。本篇報告描述其形態特徵、地理分布及生育環境，並提供彩色圖片與繪圖，同時列製檢索表以區別裸穗豬草與同屬另一歸化植物豬草(*A. artemisiaefolia* L.)。

Key words: *Ambrosia psilostachya*, taxonomy, Taiwan

關鍵詞：裸穗豬草、分類學、台灣

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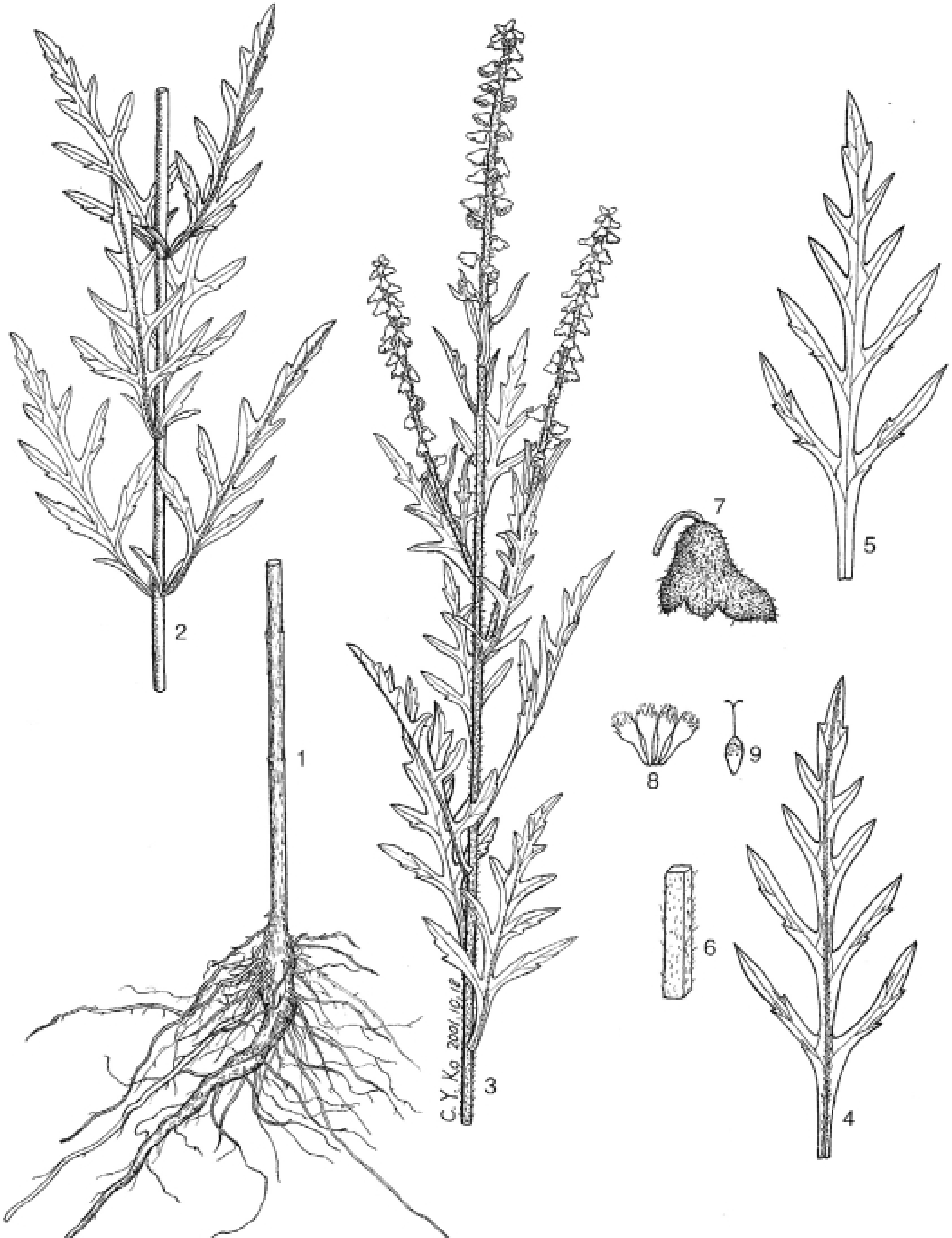

Fig. 1. *Ambrosia psilostachya* (1, roots and stem; 2, stem with leaves; 3, flowering branch; 4, lower surface of leaf; 5, upper surface of leaf; 6, stem with hairs; 7, involucre; 8, floret; 9, pistil).

圖1. 裸穗豬草的各部性狀 (1, 根部; 2, 莖部; 3, 花枝; 4, 葉背; 5, 葉面; 6, 莖的細部形態; 7, 總苞; 8, 小花; 9, 雌蕊)。

The genus *Ambrosia* L. belongs to the family Asteracea, and consists of approximately 40 species native to the New World (Britton and Brown 1970). Of them *A. artemisiaefolia* L. has been introduced to Taiwan (Hsu 1973; Peng 1998). Recently, we found that *A. psilostachya* has also established a feral population in Kaohsiung County of the southern Taiwan. We collected the specimens from Panpingshan (半屏山), Tsoying (左營), Kaohsiung Co., May 28, 2000 (Coll. No. Tseng 2350), Aug. 6, 2000 (Tseng 2557), and Aug. 19, 2001 (Tseng 2676). The specimens are deposited in the Endemic Species Research Institute Herbarium.

A. psilostachya is closely related to *A. artemisiaefolia*, but the two species are easily distinguishable; the former has pinnatifid leaves, while the latter has bi- or tripinnatifid leaves. This paper briefly describes this newly naturalized *A. psilostachya* in Taiwan, and provides with its distribution, habitat, and breeding period.

Ambrosia psilostachya DC., Sp. Pl. 102. 1753; Nagada T., Illustrated Japanese Alien Plants 254. 1972; Britton, N. L. and H. A. Brown. An Illustrated Flora of the Northern United States and Canada. 3: 266. f. 1970.

裸穗豬草 Fig.1

Erect annual or perenial herb. Stem up to 150 cm high with branched panicles in the upper half. Leaves hairy or rough on short stalks, each 5 to 12 cm long, ovate-lanceolate, deeply lobed often with toothed segments; lower leaves opposite, but upper leaves alternate. Male flowers several, not exceeding the involucre, grouped within shortly stalked hemispherical heads in terminal spike-like racemes, with up to 6-8 connate bracts forming an involucre. Corolla 4-5 mm, lilac, infundibuliform with a long tube, with 4 lobes. Calyx with 6 teeth, persistent in fruit; stamens 4, inserted on the tube of the corolla. Filament slender; anthers small, oblong, and exerted; style filiform and bifid; branches unequal. Female florets few, without a corolla, in 1-flowered heads in the axils of upper leaves; ovary 2-locular with 1 ovule in each loculus.

Fig. 2. The habitat of *Ambrosia psilostachya*.
圖2. 裸穗豬草的生育地。

Fig. 3. Plants of *Ambrosia psilostachya*.
圖3. 裸穗豬草的植株。

Fig. 4. Flowering branch of *Ambrosia psilostachya*.
圖4. 裸穗豬草的花枝。

Achene 2-7 mm, scabrid, dry with 1 seed.

Distribution: *A. psilostachya* is native to North America (Britton and Brown 1970; Bassett and Crompton 1975), and has been introduced to Japan (Nagada 1972), Germany and Spain (Takematsu and Ichizen 1987), and New South Wales of Australia from where it has spread to the eastern and southern Australia (Parsons and Cuthbertson 2002). In Taiwan it was found in Kaohsiung County.

Habitat and Ecology: *A. psilostachya* occurs in open grassland in the coastal plain of the southern Taiwan at an elevation of 220m. Its flowering period is from June to September, and the fruiting period from August to December.

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