Student Code:

24th International Biology Olympiad

第二十四屆國際生物奧林匹亞競賽

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Bern, Switzerland

BERN 2013 International Biology Olympiad

Practical Exam 4

Comparative and Functional Biosystematics

比較及功能性生物系統分類

Total points: **100**

Duration: **90 minutes**

Dear participants, 親愛的參試者

This test consists of three tasks: 本測驗包含三部分：

Please write your student code into the box on the title page.

請寫下學生考試號碼於本封面之方格中

There is no separate answer sheet. Please fill in your answers into the specific answers boxes indicated with a gray background. **Only answers given inside these boxes will be evaluated.**

本次考試無另附答案卷，請將答案填入具灰色背景之指定位置，**只有填在正確位置之答案方會記分。**

The answers have to be given either with a tick (∨) or with Arabic numbers. The numbers "1" and "7" can look very similar in handwriting. To make sure that those two numbers can be well distinguished by the IBO staff, please write them as you normally would into the following box.

答案會以打勾或阿拉伯數字顯示，數字**1**與**7**容易混淆，請務必小心書寫，為了方便計分人員辨認，請在下列方格寫下你常寫之1與7的寫法。

1 =		**7 =**	

Stop answering and **put down your pen IMMEDIATELY** when the bell rings at the end of the exam. Put the entire protocol with all the answers back into the exam envelope. Make sure you wrote your student code into the box on the title page.

當鈴聲響時，停止作答**並立刻將筆放下**。在考試結束時，將答案及試題卷全部放入所提供之封袋中。放入前請務必確認已填寫學生考號。

Material and equipment 材料與設備

Make sure that you have received all the materials and equipment listed for each task. If any of these items are missing, please raise your hand.

確實檢查每一部分進行操作時所需要的實驗器材；如有任何器材缺失，請**立刻**舉手。

Equipment 設備

1. 1 sliding caliper (150 mm) **測距游標尺**
2. 1 ruler (300 mm) 直尺
3. 1 calculator**計算機**
4. scratch paper**繪圖紙**

Skull specimen 頭骨標本

Arvicola terrestris	**arte**	European water vole 歐洲水鼠
Capreolous capreoulus	**caca**	European roe deer 歐洲小鹿
Felis catus	**feca**	domestic cat 家貓
Lepus europaeus	**leeu**	European/brown hare 歐洲棕兔
Meles meles	**meme**	European badger 歐洲獾
Sciurus vulgaris	**scvu**	Eurasian red squirrel 歐洲紅松鼠
Vulpes vulpes	**vuvu**	red fox 紅狐

Additional taxa for which data is provided

Ceratotherium simum	**cesi**	white or square-lipped rhinoceros 白(方唇)犀牛
Didelphis marsupialis	**dima**	common opossum 負子鼠
Equus ferus	**eqfe**	horse 馬
Galago senegalensis	**gase**	Senegal bushbaby 塞內加爾原猴
Genetta genetta	**gege**	common genet 小靈貓
Hippopotamus amphibius	**hiam**	hippopotamus 河馬
Inia geoffrensis	**inge**	Amazon river dolphin 亞馬遜河豚
Manis pentadactyla	**mape**	Chinese pangolin 中國穿山甲
Macropus rufus	**maru**	red kangaroo 紅袋鼠
Mustela nivalis	**muni**	least weasel 小黃鼠狼
Pipistrellus pipistrellus	**pipi**	common pipistrelle 家蝠
Procavia capensis	**prca**	rock or cape hyrax 蹄兔
Pteropus vampyrus	**ptva**	Malaysian large flying fox 馬來亞狐蝠
Sorex minutus	**somi**	Eurasian pygmy shrew 歐洲侏儒鼩鼱
Tachyglossus aculeatus	**taac**	short-beaked echidna 短吻刺蝟
Tolypeutes matacus	**toma**	southern three-banded armadillo 南方三帶犰狳

Print outs紙本資料

1. skull diagram*s* 頭骨圖

2. color print outs illustrating the presence (1) and absence (-) of the morphological characters.

   Note legend on top. 包含所有**具有(1)或缺乏(-)**的形態特徵之彩色圖，並留意圖上方之對應註記。

Introduction

Mammals, which consist of more than 5700 extant species, are omnipresent on earth and often play key roles in shaping terrestrial and aquatic ecosystems, both as predators and herbivores. Mammals are morphologically very diverse. The smallest mammals, for instance, weigh only about 2 g, whereas the blue whale, the largest animal that ever existed, is more than 100 million times larger.

哺乳類有超過**5700**種現生物種，在地球上佔有優勢，且在陸生及水生生態系中扮演關鍵角色，包括獵食者及食草者。哺乳類在形態上極具多樣化，例如最小型哺乳類僅重約兩克，而最大的藍鯨其重量為最小哺乳類體重之一億倍。

In this practical exam, you will attempt to resolve the phylogeny of some representatives of major mammal groups based on morphological characters of the skull (teeth and jaw), as well as molecular data. You will use cladistics, an approach to infer evolutionary relationships, which assumes that members of a taxonomic group have a common evolutionary history. They have therefore inherited a set of derived traits (synapomorphies) from their last common ancestor, which distinguishes members of this group from other groups.

本次實作測驗中，你必須利用頭骨(牙齒及下顎)的形態特徵以及分子生物學之資料，來解決主要哺乳動物親緣分類的問題。你將會使用支序學，這是一種用來表示演化關係之學門，其假設分類群的成員具有共同演化歷史，亦即他們自最近的相同祖先遺傳得一組衍生特徵(共同裔徵)，且藉以與其他不同群之動物成員區別。

Cladistic analysis consists of identifying specific traits and determining their state in all organisms included in the analysis. Traits can be both molecular (e.g. the specific amino acid at a specific position in a protein) or morphological (e.g. the presence or absence of a particular bone feature). The outcome of a cladistic analysis is a cladogram - a tree-shaped diagram (dendrogram) that represents the inferred phylogenetic relationships between organisms.

支序學分析包括鑑別欲分析的所有生物之生物特徵及其狀態。這些特徵可以是分子生物特徵(例如蛋白質中特殊位置的胺基酸)及形態學特徵(例如特殊骨骼特徵之具有或缺乏)兩種。支序學分析的結果是支序圖，亦即用以顯示兩物種間之親緣關係的樹狀圖表示。

Task 1: Determine presence or absence of characters [42 points]

寫出生物具有或缺乏哪些特徵(42 分)

Part 1.1 Description of morphological characters(形態特徵的描述)

The following table lists all morphological characters for which **the presence (1) or absence (-)** will be considered in this practical. Examples for each character are found on a color print out (**note the legend on top of each page**). For Characters 7 through 10, only examples of presence (1) are shown. All abbreviations given in brackets (e.g. [P]) refer to positions indicated in the skull diagrams. Note that the positions of incisors **[I]**, canines **[C]**, premolars **[P]** and molars **[M]** are enumerated from the snout to the back of the skull using superscript (upper jaw) or subscript (lower jaw). For example, **[P^3]** refers to the third premolar on the upper jaw.

下表顯示此次測驗中物種**具有(1)**或**缺乏(-)**之形態特徵。你可自所附之彩色圖表上發現各特徵之範例(請特別注意每頁上方之註記)。在特徵7至10的彩圖中，只顯示**具有(1)**此特徵者。所有縮寫顯示於中括號者(如[P])代表在頭骨圖中的位置。請特別注意在門齒[I]、犬齒[C]、小臼齒[P]、及大臼齒[M]後面之上標數字為位於上顎從頭骨前向後之次序，而下標數字為位於下顎從頭骨前向後之次序，例如[P^3]為上顎第三小臼齒。

Number	Description
1	Incisors **[I]** are present on the upper jaw. 門齒**[I]**出現於上顎
2	Elongated incisors **[I]** with abrasive (rubbed) edges indicating continuously growth through life on upper and/or lower jaw. 延長且具磨損邊緣之門齒**[I]**顯示門齒終其一生可持續在上顎或下顎生長
3	Incisors **[I]** on the front side coated with dental enamel (orange color). 門齒**[I]**在前方且其上具琺瑯質(以橘色表示)
4	Third upper incisors **[I^3]** reduced and positioned behind the second incisors. 第三上門齒(I)變小且位於第二門齒之後
5	Diastema on upper jaw. A diastema is defined as a large gap (more than two times the width of the next largest tooth) between the position of incisors **[I]** or canines **[C]** and the premolars **[P]** or molars **[M].** Some of these teeth may be absent. 上顎出現齒虛位。所謂齒虛位是指在牙齒間(例如門齒**[I]**或犬齒**[C]以及**小臼齒**[P]**及臼齒**[M]**)的無牙空位(超過鄰近此齒虛位之最大牙齒兩倍)。且可能沒有其中部分牙齒。
6	Canines **[C]** are present on the upper jaw. 犬齒**[C]**出現於上顎
7	Carnassial dentition, characterized by **[P^4]** in the upper jaw and **[M_1]** in the lower jaw forming a scissor-like structure which allows cutting and breaking, but not chewing. 食肉齒(裂齒)齒式出現：其特徵為上顎**[P^4]處**及下顎**[M_1]處**特化成剪刀狀構造，以便切斷及咬碎食物，但不能用於咀嚼。

8	Selenodont teeth, characterized by low crowns and longitudinal crescent-shaped cusps, when viewed from above. They form a series of triangular cusps when seen from the side. 新月型牙齒：當由上至下觀察時，其特徵為低齒冠且具縱走型新月狀齒冠。若由側邊觀察，可發現這些牙齒形成三角形齒冠。
9	Lophodont teeth, characterized by elongated ridges that run between cusps. Ridges are perpendicular to the jaw (like an old-fashioned washboard). 櫛狀齒冠：其特徵為兩齒冠間具有延長之隆脊。這些隆脊與上下顎相互垂直(如舊式洗衣板)
10	Teeth characterized by a well-developed V- or W-shaped ectoloph (crest). 具發育良好之 V 型或 W 型外脊(齒脊)之牙齒。
11	Pointed teeth forming conical tips. 點狀牙齒形成圓錐狀齒尖。
12	The angular extension **[Ang. Pr.]** (*Processus Angularis*) of the lower jaw is bent medial (towards the centre) and therefore more medial than **[Cond. Pr.]** *Processus condularis*). 下顎角狀延伸**[Ang. Pr.]** (*Processus Angularis*)向中間彎曲故其位置比**[Cond. Pr.]** (*Processus condularis*)較偏向中心。

Part. 1.2 Determine all character states [42 points]判斷所有特徵的狀態(42 分)

For the later analysis, it is convenient to first determine the presence or absence of each of the morphological characters considered here in each of the species included in the analysis, and to report them in the table provided in **Appedix (last page)**. Indicate presence with a “**1**” and absence with a “**-**”. **Please be extra careful when handling the skulls**. All specimens are originals and part of the collection of the Natural History Museum of Bern.

在以下之分析中，首先是去判斷本分析中所有物種之形態特徵的具有或缺乏，並將答案填在附錄(最後一頁)中所提供之表格中(每一個背景為灰色之表格皆須作答)。以**”1”表示具有該特徵，並以“-”表示缺乏該特徵。當處理及操作頭骨時請務必小心**。所有標本皆為伯恩自然科學博物館之收藏。

Task 2: Resolve phylogenetic relationships [24 points] 釐清生物的親緣關係

The goal of this task is to resolve the phylogenetic relationship among major mammalian groups. You will use two methods that will be explained in detail. In Part 2.1-2.3, you will apply the concept of maximum parsimony to the presences and absences determined in Task 1 to estimate the phylogenetic relationship between several taxa representing different major groups of mammals. In Part 2.4 – 2.5, you will use the UPGMA (Unweighted Pair Group Method with Arithmetic Mean) approach to resolve the phylogeny among Carnivora to complete a more detailed phylogeny obtained from molecular data.

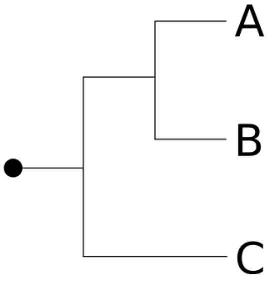
本部分之主要目的為釐清主要哺乳動物群間之親緣關係。你會使用文章中所描述之兩種方法來釐清親緣關係。在 2.1 到 2.3 部分中，你需要應用最簡約原理之概念，來分析在第一部分所得之許多不同主要之哺乳動物分類群中具有或缺乏之生物特徵，並用評估其親緣關係。在 2.4 到 2.5 部分中，使用 UPGMA(Unweighted Pair Group Method with Arithmetic Mean 無加權之數學平均值配對法)去釐清食肉目動物間之親緣關係，用來補充分子生物學資料分析而得之較精細的親緣關係。

Part 2.1: How maximum parsimony works 最大簡約法之作法

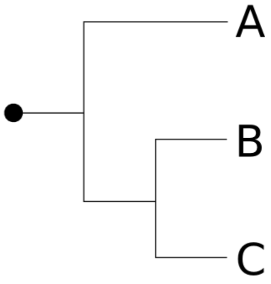
A common approach to resolve phylogenetic relationships between species is to identify the most parsimonious (the simplest) among competing phylogenies. A phylogenetic tree is called the most parsimonious if the fewest number of character state changes are invoked. To illustrate that concept, consider the following two competing phylogenies I and II for three taxa A, B and C.

最常用來釐清物種間親緣關係的方法是先找出物種間最簡約的親緣關係。最簡約的親緣關係樹是指特徵狀態改變次數最少者。為了說明此概念，請比較 A、B、C 三種不同分類群所得的 I 及 II 兩種親緣關係樹。

I



II



To choose among those phylogenies, the presence or absence of morphological characters 1 through 4 was assessed for each taxa and reported in the table below. All of these characters are known to be absent in closely related taxa, indicating that each character was absent at the root of the phylogenies (indicated by a black dot in the diagrams above).

	1	2	3	4
A	-	-	**1**	**1**
B	**1**	**1**	-	**1**
C	**1**	**1**	-	-

為選擇最適的親緣關係，各分類群的形態特徵 1 至 4 的具有或缺乏列於下表。這些特徵若在親緣最近的兩分類群中都缺乏，亦即顯示這些特徵在親緣樹根部也都缺乏(在上方樹狀圖中以黑點顯示)。

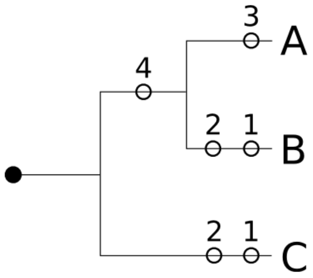
First, the minimal number of state changes has to be determined for each character and phylogeny individually. Trait 4, for instance, is present in Taxa A and B, but not in Taxon C, indicating that the state of this character changed from absent to present along the lineages leading to A and B. While this change could have happened independently on Branches A and B, the explanation leading to the minimal number of state changes (and hence the most parsimonious solution) is a single change on the branch leading to the most recent common ancestor of A and B.

首先，你應先找出每個特徵及每個親緣關係之狀態改變次數之最小值。例如特徵 4，分類群 A 與 B 中具有，但 C 分類群中缺乏，顯示這個特徵狀態在衍生成 A 及 B 的譜系上是從缺乏改變為具有。而此改變也可在 A 與 B 分支上獨立發生，由此可推得最小改變次數(即最簡約數)是在 A 及 B 的最近共同祖先分支上有一次改變。

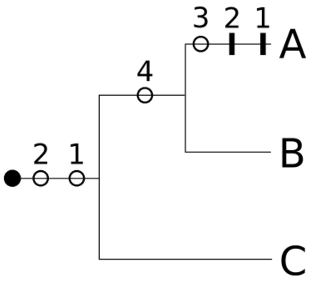
As shown in the following figure, two equally parsimonious Solutions Ia and Ib can be found for Phylogeny I when considering all characters. In Solution Ia, Characters 1 and 2 are assumed to have arisen independently on Branches B and C. Alternatively (Solution Ib), these characters arose on the branch coming from the root of the phylogeny, and were lost on the Branch A. Note that throughout this practical, **open circles indicate gains** (changes from absent → present) and **black bars indicate losses** (state changes from present → absent).

當包含所有特徵時，親緣關係樹 I 有同等簡約的結果 Ia 及 Ib(如圖所示)。在 Ia 中，特徵 1 與 2 在兩分支 B 與 C 上獨立改變。然而在 Ib 中，這兩個特徵源自親緣關係樹根部，然後又在分支 A 中喪失。然後又在請注意在此實作題中，空白圓圈顯示此特徵之獲得(從缺乏改變為具有)，而黑色條狀圖表示此特徵喪失(從具有改變為缺乏)。

Ia



Ib

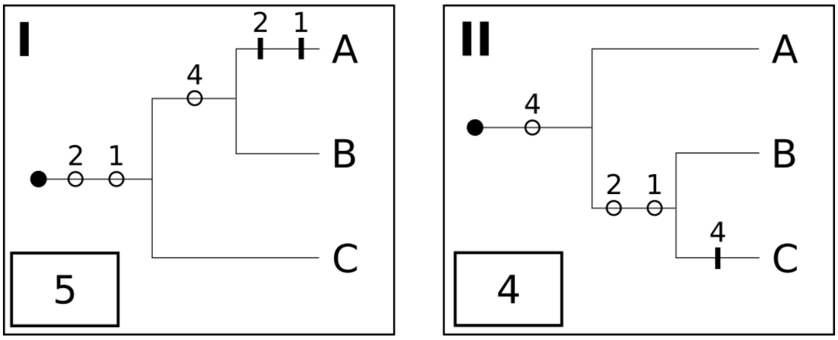


A key observation is that any character for which the state in a single taxon differs from the state at the root (such as Trait 3 in this example) invokes a single character change, regardless of the phylogeny considered. Such characters and those for which the state is identical in all taxa should be regarded as uninformative and discarded prior to the analysis.

關鍵性的觀察是:不論是哪個親緣關係，任何一個僅發生在單一分類群的改變，且其狀態與親緣關係樹的根部不同，如特徵 3。此類廣泛出現於所有分類群之相同特徵，即視為無法提供有效資訊之特徵，且應在分析前即捨棄不用。

The following figure finally shows one of the most parsimonious solutions for each of the competing phylogenies, along with the number of character state changes invoked by these solutions given in the box. Thus, under the concept of maximum parsimony, Phylogeny II is chosen as the best estimate of the true phylogenetic relationship between Taxa A, B and C.

在最後下圖顯示每個親緣關係樹分析而得的最簡約樹。其特徵改變次數標示於方格中。所以，根據最簡分析原理，親緣關係樹 II 可視為分類群 A，B，C 三者間之親緣關係之最佳估計方式。



Part 2.2: Resolve the phylogenetic relationship using parsimony [10 points]

利用簡約法來釐清親緣關係

You will now use maximum parsimony to resolve the phylogenetic relationship among the following taxa, representing a major mammal clade:
使用最大簡約原理來釐清以下主要哺乳動物分類系之親緣關係：

- *Arvicola terrestris* (**arte**)
- *Ceratotherium simum* (**cesi**)
- *Equus ferus* (**eqfe**)
- *Genetta genetta* (**gege**)
- *Lepus europaeus* (**leeu**)
- *Capreolus capreolus* (**caca**)
- *Sorex minutus* (**somi**)

First, indicate with a tick (√) if Characters 1 through 12 (page 5) are informative to resolve the phylogeny of these taxa, or not. Note that all characters are known to be absent at the root of these taxa, with the **exception of 1, 6 and 11, , which are present at the root**.

首先，請勾選(√)特徵 1 到 12 中是否為有助於釐清這些分類群中親緣關係之有用或者無用之資訊。請注意：**除了出現於親緣關係樹基部之特徵 1、6 與 11** 外，這些特徵在分類群的根部之狀態為缺乏。

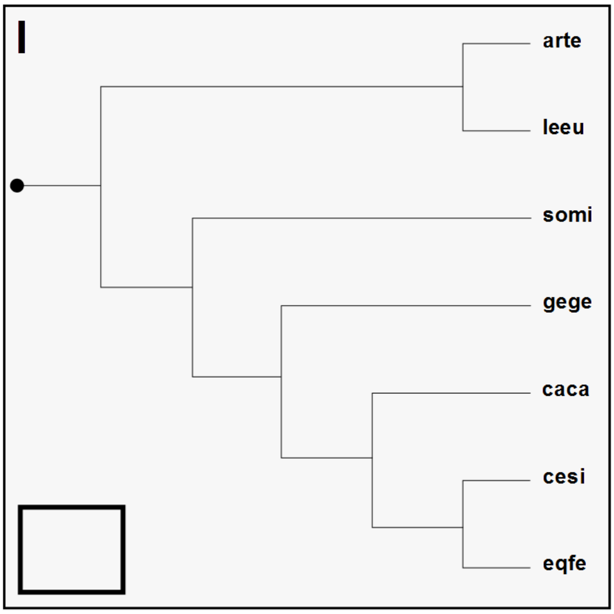
Q2

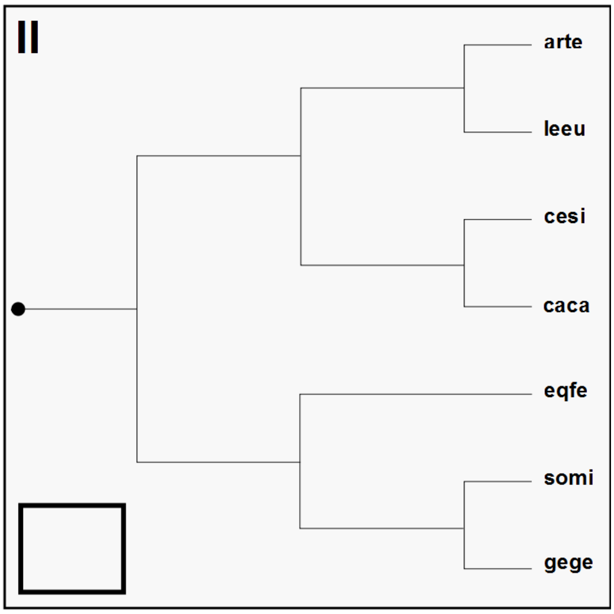
Character(特徵)	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Informative 可提供相關資訊												
not informative 不可提供相關資訊												

Next, indicate any of the most parsimonious solutions regarding character state changes for each of the two competing phylogenies I and II directly into the figure. Indicate **gains with empty circles and losses with bars** and write the number of the corresponding characters above it. Finally, indicate the total number of state changes necessary in the box provided.

接下來，分別在親緣關係樹 I 與 II 上標出最簡約的改變情況，以空白圓圈代表獲得，而條狀代表喪失該特徵，並請在其上寫下相對應特徵之數目字(如之前所舉之例子)。最後，寫下所有改變的總次數於所提供之方格中。

Q3





Indicate the phylogeny that represents the best estimate of the true phylogenetic relationship among those 7 taxa according to the concept of maximum parsimony with a tick (√) in the table below

根據最簡約原理，請於下表勾選(√)最適於代表上述七個分類群之親緣關係樹

		I	II
Q4	Preferred phylogeny according to the concept of maximum parsimony 利用最大簡約原理顯示之最適親緣關係樹		

Part 2.3: Identify characters reflecting diet [4 points] 判斷可反應攝食方式的特徵(四分)

Unless a large number of characters are included, maximum parsimony is often too simplistic an approach to correctly disentangle the phylogeny of distantly related taxa. This is particularly true when some character state differences between taxa reflect opposing adaptations to diet rather than a phylogenetic signal. To evaluate this hypothesis, identify the characters that are typical for either an carnivorous or a herbivorous lifestyle.

若無大量特徵所提供之資訊，最大簡約法可能會過於簡化而無法正確釐清兩個關係較遠的分類群之親緣關係。此種失誤尤其會出現在因飲食而非親緣訊息所造成之相反適應的現象。為了評估此假說，請鑑別食肉性及食草性動物生活型態之特徵。

Among the species included in this practical, the following are very distantly related but are highly carnivorous and prey on living Arthropoda, Mollusca, Annelida and/or Vertebrata:

在此實作題所提供之下列物種，其彼此間親緣關係並不密切，但都是高度肉食性之動物且獵食多種生物如節肢動物，軟體動物，環節動物或(及)脊椎動物:

- *Didelphis marsupialis* (**dima**)
- *Galago senegalensis* (**gase**)
- *Inia geoffrensis* (**inge**)
- *Mustela nivalis* (**muni**)
- *Pipistrellus pipistrellus* (**pipi**)
- *Sorex minutus* (**somi**)
- *Tolypeutes matacus* (**toma**)

The following are very distantly related species but are known to be highly herbivorous and feed on grass, leaves, fruits and roots:

下列物種間的親緣關係較遠，但皆為高度草食性且多攝取草，樹葉及植物根部。

- *Arvicola terrestris* (**arte**)
- *Capreolous capreolus* (**caca**)
- *Equus ferus* (**eqfe**)
- *Lepus europaeus* (**leeu**)
- *Macropus rufus* (**maru)**
- *Procavia capensis* (**prca**)
- *Pteropus vampyrus* (**ptva**)

Indicate with a tick (√) in the table below for each Character 1 through 12 whether its presence or absence is typical for either an carnivorous or herbivorous lifestyle. Here, a typical character state is defined as any character state shared by at least three of the taxa from one of the two groups but absent from all members of the other group.

在下表特徵 1 到 12 中，從典型肉食性動物及草食動物生活型態，勾選(√)出可表現具有或缺乏狀態之典型特徵。請注意所謂典型特徵狀態指的是在一群動物中至少三種分類群為具有，而在另一群動物中則為缺乏。

Q5

Character 特徵	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
typical for animalivores 肉食性動物之典型特徵												
typical for herbivores 草食性動物之典型特徵												
not typical for either 在兩種動物皆非典型特徵												

Part 2.4: How UPGMA works (UPGMA 如何作用)

An approach that is purely based on the presence or absence of morphological characters does not lend itself readily for estimating evolutionary distance between taxa quantitatively. This is where molecular data, which provides a large set of characters with similar state change probabilities, becomes very handy. A simple, iterative approach to estimate a phylogeny along with the relative length of each branch from molecular data is UPGMA (Unweighted Pair Group Method with Arithmetic Mean), in which the pair of clusters with the shortest distance is combined into a higher level cluster at each iteration.

僅憑形態特徵具有或缺乏，無法量化分類群之演化距離。所以，可提供大量具相似狀態變化概率資訊之分子生物學數據就變得十分重要。而 UPGMA(Unweighted Pair Group Method with Arithmetic Mean 無加權之數學平均值配對法)就是一種簡單，可重覆的方法，用以估算每一演化分支之相對距離及其親緣關係，在 UPGMA 分析中，可將具最短距離的群(cluster)合併為更高一階的群。

To illustrate that concept, consider the molecular distances (e.g. number of base pair differences) between the Taxa A, B, C and D.

為了說明此種概念，請考慮分類群 A、B、C、D 中之分子距離(例如鹼基對之數目)

	A	**B**	**C**	**D**
A	0			
B	6	0		
C	7	8	0	
D	8	9	4	0

Iteration 1: First, the pair of clusters with the smallest distance is the pair C and D, which is combined into a higher-order cluster (C,D). The relative age of the newly formed cluster is computed as half of the distance between the two clusters combined. In this case, the relative age of the cluster is thus 2.

整併一:首先，成對物種 C 與 D 間之分子距離最短，可合併為一較高階之分類群(C,D)；而此種新形成之分類群之相對距離則可利用其分子距離之半數來計算。在此例中，此分類群之相對距離數值為 2。

Next, a new matrix of all distances is generated by computing the distance between clusters as the average distance between all taxa from one cluster to all taxa of the other cluster. The distance between cluster A and cluster (C,D), for instance, is computed as the average between d(A,C) and d(A,D), where d(x,y) is a notation to indicate the distance between clusters x and y.

接下來，所有距離所形成之新矩陣可藉由計算兩兩分類群(cluster)的距離(即兩個分類群所含之所有物種距離之平均值)。例如物種群 A 及分類群(C,D)間的距離是 d(A,C)及 d(A,D)的平均，其距離數值 d(x,y)可用以標示物種群 X 及 y 之演化距離。

	A	**B**	**(C,D)**
A	0		
B	6	0	
(C,D)	7.5	8.5	0

Iteration 2: The pair of clusters with the smallest distance is now the pair of A and B, which is thus combined into a higher level cluster (A,B) with a relative age of 3. Again, distances are recomputed as indicated above. The distance d((A,B),(C,D)) is thus the average between d(A,C), d(A,D), d(B,C) and d(B,D), which is the same as the average between d(A,(C,D)) and d(B,(C,D)).

整併二：此時，具最短距離之成對分類群為 A 與 B，這兩者可合併為較高階的分類群(A，B)，而其相對距離為 3。同樣的方法可用以計算兩者間距離。兩較高階分類群之相對距離[d((A,B),(C,D)]為 AC 間距離 d(A,C)，AD 間距離 d(A,D)，BC 間距離(d(B,C)及 BD 間距離 d(B,D)之平均值，其值等同於 A 與較高階分類群(C,D)[d(A,(C,D)]及 B 與較高階分類群(C,D)[d(B,(C,D)]之平均值。

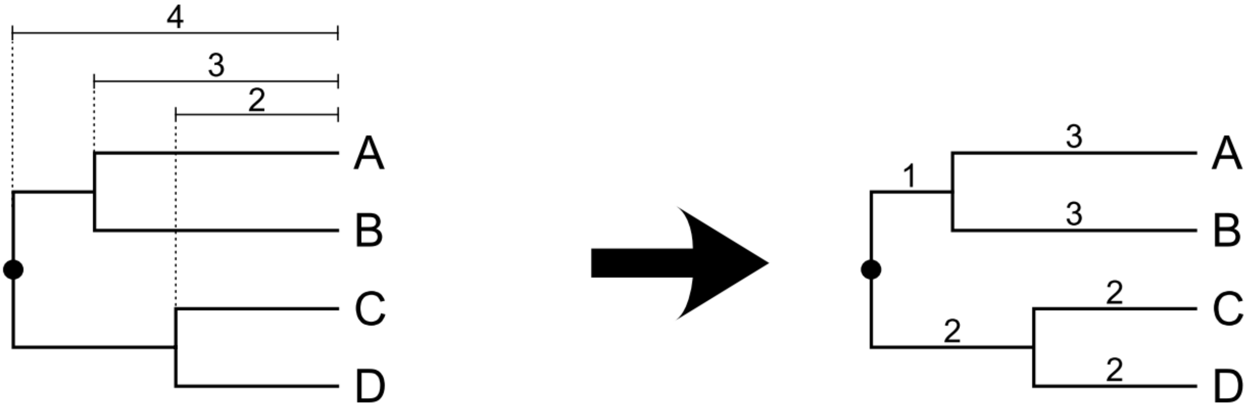
	(A,B)	**(C,D)**
(A,B)	0	
(C,D)	8	0

Iteration 3: In the last iteration, the two remaining taxa are combined into the new cluster ((A,B),(C,D)) and the relative： age of this cluster is 4.

整併三：在最後兩種剩下的分類群又可合併為新的高階分類群((A,B),(C,D))，而此新的較高分類群之平均相對距離為 4。

Computing branch length: After all taxa have been combined into a single cluster, the resulting tree is plotted with the relative age of each cluster. From these relative times, it is then straight forward to compute individual branch length.

計算分支長度：當所有分類群皆合併為一個高階分類群，可利用各較高分類群之相對距離繪製出一個樹狀圖。經由這些相對的時間整併數，可計算出個別分支的長度。



Part 2.5: Resolve the phylogenetic relationship using UPGMA [10 points]

如何利用 **UPGMA** 來釐清親緣關係(**10** 分)

Resolve the phylogenetic relationship of all five Carnivora species included in this practical iteratively using the UPGMA method. Standardized molecular distances between all pairs of these taxa are given in the table below.

請利用 UPGMA 的方法來釐清此實作題所包括之五種食肉目動物的親緣關係。下表所提供的是成對分類群之標準化的分子距離數值。

Vuvu	*Vulpes vulpes*
Muni	*Mustela nivalis*
gege	*Genetta genetta*
meme	*Meles meles*
feca	*Felis catus*

	A	**B**	**C**	**D**	**E**
A	0.00				
B	4.18	0.00			
C	4.96	4.96	0.00		
D	4.18	0.48	4.96	0.00	
E	4.96	4.96	2.82	4.96	0.00

Proceed iteratively and always fill in the table with the molecular distances considered. Make sure to always report the code of the cluster in the top and left most row. Use the notation introduced above to denote higher level clusters. The term ((x,y),z), for instance, should refer to a cluster made of the clusters (x,y) and z. Also, report the relative age of the newly formed cluster in each iteration (precision: two digits after the decimal point).

反覆運算並在答案表中填入分子距離。確認要在行列處寫上分類群代碼。並利用上述之表示方式顯示較高之分類群。舉例來說，((x,y),z)表示由分類群(x,y)及 z 所組成之較高分類群。同時，寫出每一整併過程新形成之較高階分類群之相對距離(請寫至小數點後第二位)。

Iteration 1(整併一)

Q6

	0.00			
		0.00		
			0.00	
				0.00

Relative age of newly formed cluster(較高階分類群之相對距離)

Iteration 2(整併二)

Q7

	0.00		
		0.00	
			0.00

Relative age of newly formed cluster(較高階分類群之相對距離)

Iteration 3(整併三)

Q8

	0.00	
		0.00

Relative age of newly formed cluster(較高階分類群之相對距離)

Iteration 4(整併四)

Q9

Relative age of newly formed cluster(較高階分類群之相對距離)

Now draw the resulting phylogeny of the five species to scale and indicate the length of each branch on the top and the species code on the right of it. Note that 5 mm indicates 0.1 unit of relative age of your calculated tree.

現在請描繪出五種物種之親緣關係，以刻度計量並標示每一分支之相對距離於分支上方而物種代號標示於其右方(如之前圖例)。請注意，以 5mm 為你所計算出之樹狀圖上之相對距離的 0.1 單位。

Q10

Task 3: Rate of morphological evolution [34 points] 形態演化的速度

If morphological changes happen at a constant rate, the morphological difference between pairs species measured at multiple characters should be highly correlated with the phylogenetic distance between the species as estimated from molecular data. In this task, you will test this hypothesis by using a series of skull measurements. While the results are provided for many additional species pairs, you will perform the necessary measurements and calculations for the species pair *Arvicola terrestris* (**arte**) and *Lepus europaeus* (**leeu**).

如果形態改變以一恆定速率發生，以多項特徵所測得之兩兩物種間的形態區別，應該與從分子資料所估計的物種間親緣距離高度相關。在此實驗部份，請用一系列的頭骨測量來測試此一假說。雖然結果中提供許多其他物種對，你應執行對歐洲水鼠(arte)和歐洲棕兔(leeu)物種對的必要測量與計算。

Part 3.1: Obtain necessary skull measurements [15 points]

獲取必要的頭骨測量值(15 分)

The table below indicates a series of skull features which you will have to measure for the two species mentioned above. All measurements are also indicated in the skull diagrams.

下表顯示前面提到的兩應測量物種的頭骨系列特徵。所有測量結果也在頭骨關係圖中顯示。

	Description
M_1	distance in mm between **[I^1]** and **[NF1]**. **[I^1]** and **[NF1]**間之距離以 mm 表示
M_2	distance in mm between **[Ang. Pr.]** and end of masseter depression (masseter muscle attachment point). **[Ang. Pr.]**與嚼肌下沉之末端(嚼肌接觸點)
M_3	distance in mm between **[Ang. Pr.]** and **[Cond. Pr.]**。 **[Ang. Pr.]** and **[Cond. Pr.]**. 間之距離以 mm 表示。
M_4	distance in mm between **[I]** and **[Cond. Pr.]**。**[I]** and **[Cond. Pr.]** 間之距離以 mm 表示
M_5	distance in mm between end of eyes and end of **[PA]** 。**[PA]**末端至眼睛末端之距離以 mm 表示
M_6	distance in mm between eyes and **[PMX]**. **[PMX]**與眼睛間之距離以 mm 表示
M_7	distance in mm between **[PMX]** or **[NA]** or **[I]** and **[Cond. Pr.]**. **[PMX]**或**[NA]**或 **[I]**與**[Cond. Pr.]** 間之距離以 mm 表示。

While results for features M_5 and M_6 will be provided below, measure the five features (M_1 through M_4 and M_7) for both specimens (**arte** and **leeu**). Focus on the right side of the skull (the left side when facing the skull). Report your results in mm in the table to a precision of 0.1 mm

下表提供 M_5 和 M_6 的結果，寫出該二物種（**arte** 和 **leeu**）其他的五個測量值（M_1 到 M_4 以及 M_7）。請著重在頭骨的右側(正對頭骨時，在你的左側)。在下表中以 mm 為單位寫出你的結果，並精準到 0.1 mm。

Q11

	M_1	M_2	M_3	M_4	M_5	M_6	M_7
arte *Arvicola terrestris*							
leeu *Lepus europaeus*							

Part 3.2: Calculate the morphological distance between species pairs [15 points]

計算二物種對間的形態距離(15 分)

A major hurdle when studying different skull features is that they are primarily determined by the overall size of the specimen. To study skull shape, begin by correcting for the overall size of the skull by dividing each measurement by the length of the skull (M_7) and taking the logarithm to base 10 from this ratio. For each measurement $M_i = \{M_1, ..., M_4\}$, calculate:

在研究不同頭骨特徵時的一個主要困難，是它們會受樣本個體體型大小的影響。為研究頭骨形狀，須先作該一頭骨個體體型大小的校正，將每個測量值除以頭骨長度(M7)後，並取其以 10 為底數的對數值。對每個測量值，$M_i = \{M_1, ..., M_4\}$，請計算：

$$\widehat{M}_i = \log_{10}\left(\frac{M_i}{M_7}\right)$$

Report your results in the table below with a precision of three digits after the decimal point.

在下表中寫出你的結果，並精準到小數點後第三位。

Q12

	$\widehat{M}_1$	$\widehat{M}_2$	$\widehat{M}_3$	$\widehat{M}_4$	$\widehat{M}_5$	$\widehat{M}_6$
arte *Arvicola terrestris*					-0.367	-0.478
leeu *Lepus europaeus*					-0.547	-0.382

Next, compute the absolute morphological distance $d_i(x,y)$ between the two species *x* and *y* for each measurement *i* as

其次，計算 x 及 y 二物種間 *i* 的絕對形態距離$d_i(x,y)$：

$$d_i(x,y) = \left|\widehat{M}_i(x) - \widehat{M}_i(y)\right|$$

where $\widehat{M}_i(x)$ is the standardized measure *i* of species *x*. The absolute difference is the difference regardless of whether it is negative or positive. Report your results with a precision of three digits after the decimal point in the table below.

其中的$\widehat{M}_i(x)$代表物種 x 的標準化測量 *i*。絕對差異是不考慮正負數，亦即為絕對值。在下表中寫出你的結果，並精確到小數點後第三位數。

Q13

	$d_1(x,y)$	$d_2(x,y)$	$d_3(x,y)$	$d_4(x,y)$	$d_5(x,y)$	$d_6(x,y)$
arte and **leeu**						

When combining the different measures into a single distance, it is important to first standardize the distances in order to give them equal weight. A simple procedure to standardize is to divide the absolute differences $d_i(x,y)$ by the median difference $\tilde{d}_i$ across all species pairs considered:

當要將不同的測量法組合到單一距離時，重要的是要先將距離標準化，使其能有同等權重。一個標準化的簡單過程是將絕對差異 $d_i(x,y)$ 除以跨所有物種對的中位數差 $\tilde{d}_i$：

$$\hat{d}_i(x,y) = \frac{d_i(x,y)}{\tilde{d}_i}$$

The appropriate medians are indicated in the table below. 各適當的中位數如下表中所示：

$\tilde{d}_1(x,y)$	$\tilde{d}_2(x,y)$	$\tilde{d}_3(x,y)$	$\tilde{d}_4(x,y)$	$\tilde{d}_5(x,y)$	$\tilde{d}_6(x,y)$
0.084	0.139	0.067	0.026	0.110	0.082

Standardize all distances and report your results with a precision of three digits after the decimal point in the table below.

將你所有結果間距標準化，並在下表中寫出結果，並精確到小數點後第三位。

Q14

	$\hat{d}_1(x,y)$	$\hat{d}_2(x,y)$	$\hat{d}_3(x,y)$	$\hat{d}_4(x,y)$	$\hat{d}_5(x,y)$	$\hat{d}_6(x,y)$
arte and **leeu**						

The combined morphological distance $D(x,y)$ of a pair (*x*,*y*) is defined as the sum across all standardized distances of that pair:

現在每對(*x, y*)之綜合形態距離 *D*(*x, y*)，即為該配對所有標準化距離的總和

$$D(x,y) = \sum_{i=1}^{6} \hat{d}_i(x,y)$$

Calculate $D(x,y)$ for arte and leeu and report your results with a precision of three digits after the decimal point in the table below.

計算兩物種間(arte 及 leeu)之綜合形態距離 *D*(*x, y*)，並在下表中寫出你的結果，並精確到小數點後第三位。

Q15

	$D(x,y)$
arte and **leeu**	

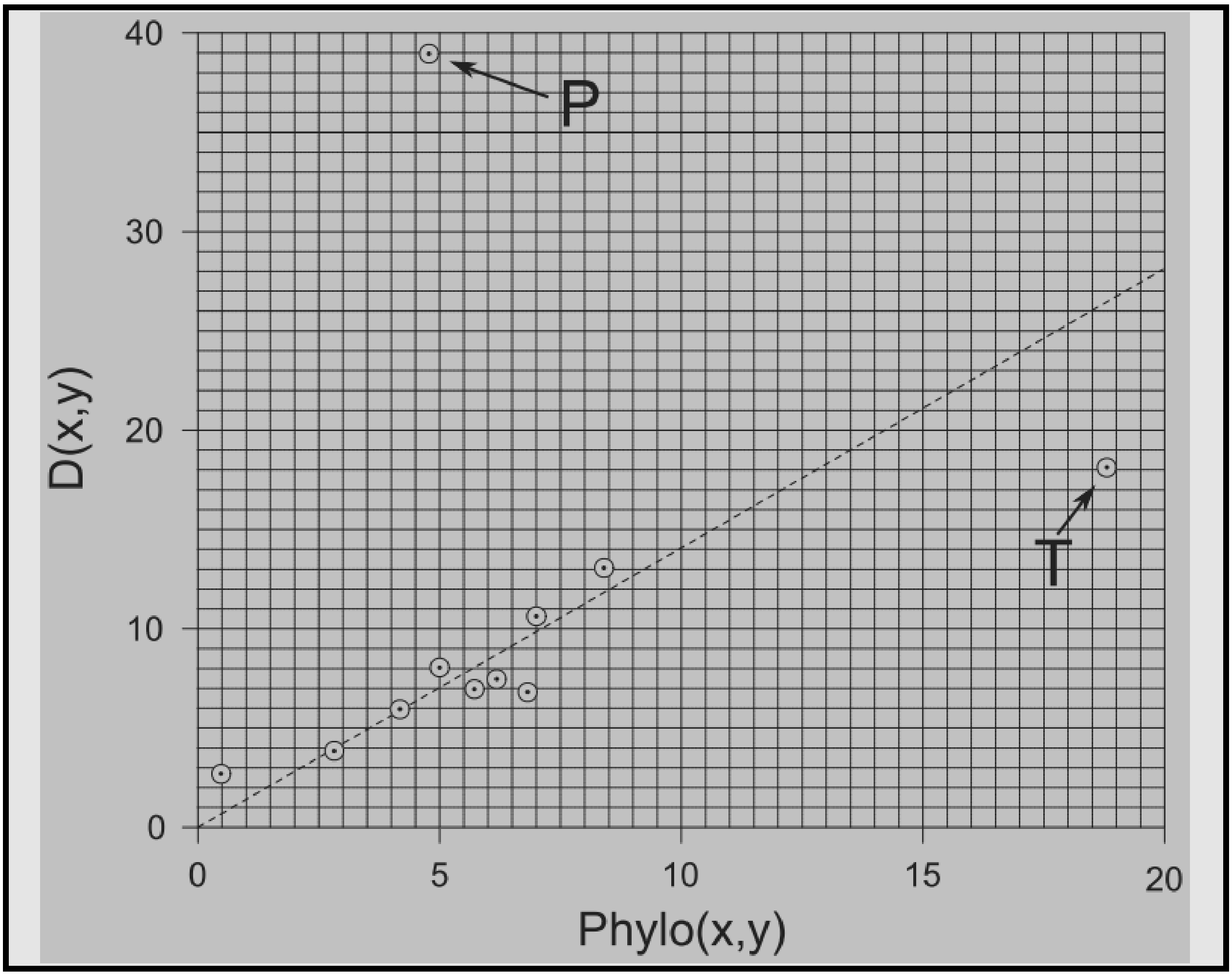
Part 3.3: Plot the phylogenetic versus the morphological distance [2 points]

繪製系統發生對形態距離關係圖

The graph below shows the phylogenetic distance $Phylo(x, y)$ against the morphological distance $D(x, y)$ for pairs of some of the species listed in the Appendix, along with a linear regression best explaining the observed values. Add your calculated distances to this plot by using a dot with a circle around, similar to the other points. The phylogenetic distance between **arte** and **leeu** is 6.80.

下圖顯示在附錄中列出的某些物種對，其系統發生距離$Phylo(x, y)$對形態距離$D(x, y)$的相關性，其線性回歸是觀察值的最佳解釋。將你所計算的距離用一個周圍有圓圈的點(比照其他點)加入此圖中。arte 和 leeu 間的親緣距離為 6.80。

Q16



Part 3.4: Interpret the results [2 point] 結果解釋[2 分]

The plot of the phylogenetic versus the morphological distance shows two obvious outliers, points P and T. Indicate with a tick (√) for each of the following hypotheses whether it could explain these outliers or not.

在系統發生對形態距離關係圖中有 P 和 T 兩個明顯的異常值，針對下列各假說是否可以解釋這些異常值，請打勾(√)與正確位置。

Q17

	yes	no
Both species of pair P are closely related but were geographically separated and evolved convergent adaptations to very similar habitats. P 配對的兩個物種親緣相近但地理分離，向非常相似的棲地趨同演化。		
The ancestor of one species of pair P colonized a totally different environment with very different selection pressures, changing its skull morphology dramatically. P 配對中一個物種的祖先拓殖到基本選擇壓力完全不同的環境，導致其頭骨形態有戲劇化的改變。		
Both species of pair T are part of a fast, ecologically driven adaptive radiation. T 配對的兩個物種均為一快速、生態驅動適應性輻射的一部分。		
While only distantly related, both species of pair T feed on very similar resources, for which their skulls evolved convergent adaptations. 雖然只是遠親，T 配對的兩個物種有非常相似的食物來源，其頭骨有趨同演化。		

End of practical exam

實作考試至此結束

Appendix: Character states (presence or absence) of all specimens

附錄：所有標本之生物特徵狀態(具有或缺乏)

Presences are indicated with a “1” and absences with a “-”.具有之特徵請以“**1**”表示；而缺乏之特徵以“**-**”表示。

Q1

Character		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
arte	*Arvicola terrestris*												
caca	*Capreolus capreolus*												
feca	*Felis catus*												
leeu	*Lepus europaeus*												
meme	*Meles meles*												
scvu	*Sciurus vulgaris*												
vuvu	*Vulpes vulpes*												
cesi	*Ceratotherium simum*	-	-	-	-	1	-	-	-	1	-	-	-
dima	*Didelphis marsupialis*	1	-	-	-	-	1	-	-	-	-	1	1
eqfe	*Equus ferus*	1	-	-	-	1	1	-	-	1	-	-	-
gase	*Galago senegalensis*	1	-	-	-	-	1	-	-	-	-	1	-
gege	*Genetta genetta*	1	-	-	-	-	1	1	-	-	-	1	-
hiam	*Hippopotamus amphibius*	1	1	-	-	-	1	-	-	1	-	-	-
inge	*Inia geoffrensis*	-	-	-	-	-	-	-	-	-	-	1	-
mape	*Manis pentadactyla*	-	-	-	-	-	-	-	-	-	-	-	-
maru	*Macropus rufus*	1	1	-	-	1	-	-	-	1	-	-	1
muni	*Mustela nivalis*	1	-	-	-	-	1	1	-	-	-	1	-
pipi	*Pipistrellus pipistrellus*	1	-	-	-	-	1	-	-	-	1	1	-
prca	*Procavia capensis*	1	1	-	-	1	-	-	-	1	-	-	-
ptva	*Pteropus vampyrus*	1	-	-	-	-	1	-	-	-	-	-	-
somi	*Sorex minutus*	1	-	-	-	-	1	-	-	-	1	1	-
taac	*Tachyglossus aculeatus*	-	-	-	-	-	-	-	-	-	-	-	-
toma	*Tolypeutes matacus*	-	-	-	-	1	-	-	-	-	-	1	-