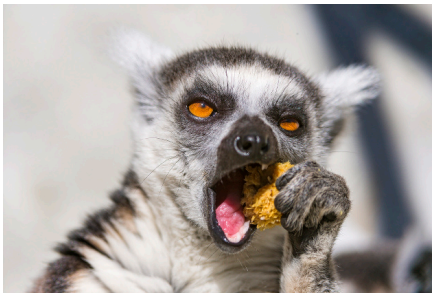
Survey for Feedback: **http://goo.gl/tLw7sE**



Straight from the Lemur's Mouth:

Exploring dietary adaptation and evolutionary relationships using lemur teeth

Duke UNIVERSITY

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Summary

Students will examine digital models of teeth from 10 lemur species. They will form hypotheses as to the diets and evolutionary relationships of these lemurs from an analysis of their dental morphology. They will then compare their hypotheses to information on the dietary ecology of wild lemurs and to a phylogenetic tree derived from genetic information. They will be evaluated on their ability to articulate whether and how their hypotheses differ from this external information, drawing on what they have learned about the interpretation of phylogenetic trees and the interacting impacts of dietary adaptation and shared evolutionary history on tooth shape. An optional final activity will have students form hypotheses about the dietary adaptations and relationships of extinct lemurs and evaluate these through an investigation of the primary scientific literature.

Materials

- Computer or tablets for groups of 3-5 students and teacher
- Paper and pencil for students
- Projector for teacher

Duration

- **1-1.5 hour**

Grade Levels

- 9-12

Setting

- Indoor classroom or computer lab

Objectives

- Use information on dietary adaptation to interpret the shapes of lemur teeth in adaptive terms
- Articulate a hypothesis of evolutionary relationships from morphological information
- Evaluate this hypothesis by correctly interpreting a phylogenetic tree constructed from genetic information

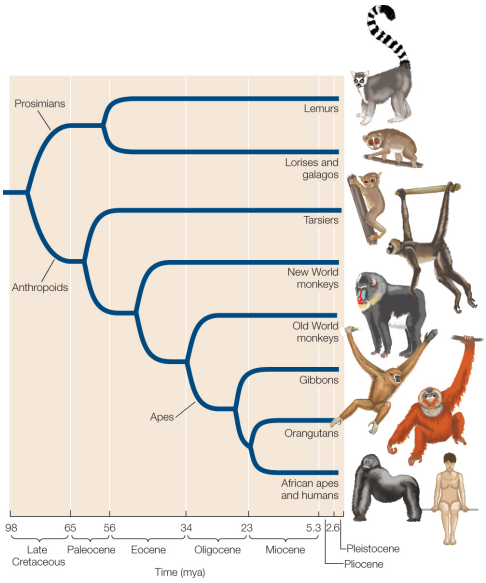
North Carolina Essential Standards

- EX.Bio.1.2
- Bio.2.12
- Bio.3.3.1
- Bio3.4.1
- Bio.3.5.2
- Bio.2.2.1

Background Materials

Lemur Evolution

Figure 1 - Lemurs in a primate phylogeny



Lemurs (Lemuriformes) are one of two groups of living strepsirrhine primates, the other (Lorisiformes) including bushbabies, lorises, and relatives. Humans are in the other large grouping called the haplorrhine primates, which we share with monkeys, tarsiers, and the other apes. Humans and likely shared a common ancestor over 60 million years ago. Modern lemurs evolved in apparent isolation on the island of Madagascar over the last 50 million years.

They have become remarkable diverse, with different species eating everything from grubs to nectar to leaves to lichen, and moving around through every means from careful climbing along tree branches to acrobatic leaping between spiky euphorbs. Some lemurs have become extremely specializing, most spectacularly exemplified by the aye-aye (*Daubentonia madagascariensis*), which has evolved rodent-like dentition but appears to feed most like a woodpecker, probing tree limbs for grubs which are extracted by gnawing. Several species of lemur became extinct within the last 10,000 years, likely due to human activities. These included the largest lemurs, which approached the size of female gorillas, and lemurs with unusual sloth-like adaptations.

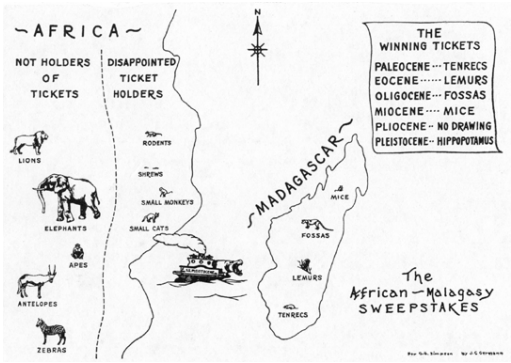


Figure 2 - Mammalian dispersals to Madagascar

Lemurs are of special interest to scientists for several reasons. The first is their remarkable diversity, which appears to represent a case of “adaptive radiation,” a pattern of evolution where-by very rapid adaptive change accompanies the exploitation of new habitats, as in the finches of the Galapagos. Lemur social behavior is also of interest to primatologists, as most social lemurs have female-dominated groups, unusual for primates. Finally, the lemur faunas of Madagascar represent the best analogy for the primate faunas of the other continents around 40 million years ago during the Eocene.

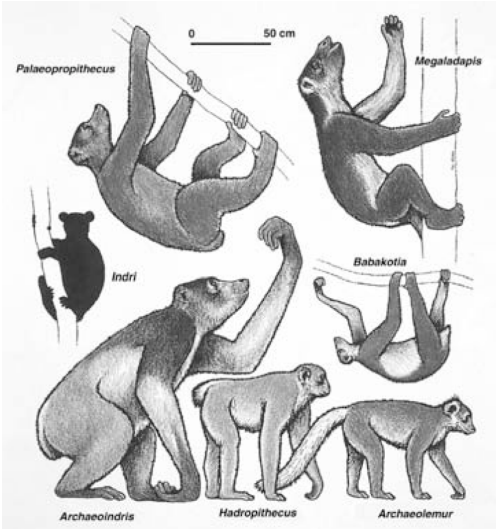


Figure 3 - Subfossil lemurs

Tooth shape

Several methods have been devised to describe tooth shape and test for its relationships to dietary adaptation. All of them agree that teeth with a greater number of sharp crests are associated with the processing of more fibrous, tough foods than teeth with more rounded surfaces. In primates, this is generally leaves or insects, which, interesting, share many of the same material properties. Body size is generally necessary to distinguish leaf- from insect- eating primates as energetic efficiency considerations necessitate very large lemurs (> 500 g) to consume primarily leaves to meet both their protein and calorie requirements. Almost all primates are omnivorous, however, and most rely extensively on fruit for calories. All of the lemurs used in this exercise eat a mix of leaves, fruits, and other plant parts, as well as occasional insects. The categories “frugivory” and “folivory” refer to the primary adaptive pressure shaping their teeth, not an exclusive dietary dependence.

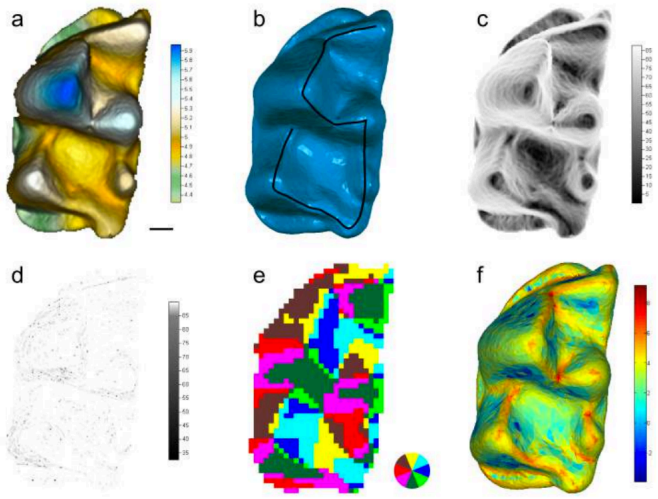


Figure 4 - Six methods for measuring tooth surface shape (Tooth height, shearing edge length, slope, angularity, orientation patch count, Dirichlet normal energy)

Activity Overview

Engage

Begin the lesson with a video introduction to lemurs and the challenges they face from the American Museum of Natural History: https://youtu.be/JB5r2_Yxnj0. Several lemurs that the students will see in the exercise are featured (in order of first appearance: indri (0:17), sifaka (1:39) [not in lesson, but a relative of indris and wooly lemurs], wooly lemur (1:46), brown lemur (1:52), bamboo lemur (1:59), ring-tailed lemur

(2:04), mouse lemur (2:08). If students have visited the Duke Lemur Center, point out that sifakas, brown lemurs, bamboo lemurs, ring-tailed lemurs, dwarf lemurs, mouse lemurs, and ruffed lemurs can all be seen there.

Direct students to the “Straight From the Lemurs Mouth” project on Morphosource (http://www.morphosource.org/Detail/ProjectDetail/Show/project_id/598) where they will be able to view the teeth used in the lesson. Alternatively, teeth may be 3D printed from downloaded files if this is available. Have students form hypotheses as to the dietary behavior of each of the living lemur species (*Archaeolemur*, *Babakotia*, and *Megaladapis* excluded) from the shapes of the teeth, and record them using the worksheet provided.

Explore

Reveal the true lemur diets. Discuss in class which species were the most difficult to classify, pointing out taxa that eat both fruits and leaves (*Lemur catta*) and that eat insects (*Microcebus*). Suggest that the evolutionary history of some of the lemurs might also make the activity more difficult, as more closely related animals are more likely to resemble one another. On a sheet of paper, have groups form hypotheses as to the evolutionary relationships of the living lemurs. They may represent these relationships any way they like, but must include all of the taxa.

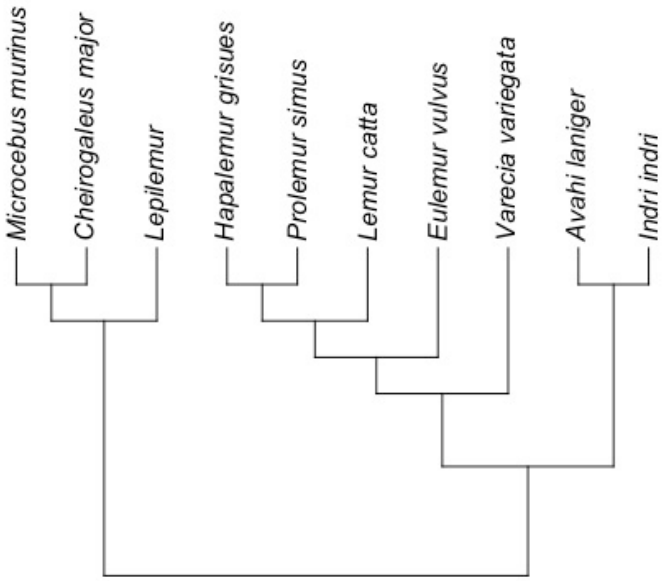
Explain

Explain the relationship between tooth shape and dietary adaptation in more detail, drawing in differences in average food material properties between different diets. Explain how this is an example of adaptation, with different lemur species evolving to most efficiently exploit different diets to avoid direct competition.

Distribute tree-reading worksheet and go over examples, translating a family tree into a phylogeny and presenting the phylogeny of primates. Optionally, use some of the tree thinking exercises from Baum et al. 2005 to further explore tree reading.

Elaborate

Show the students the tree of relationships of living lemurs as determined from genetic evidence (below). Briefly explain how the tree was constructed (using sequences of DNE, particularly focused on regions that don’t encode functional traits and so aren’t as prone to convergence as functional structures like teeth).

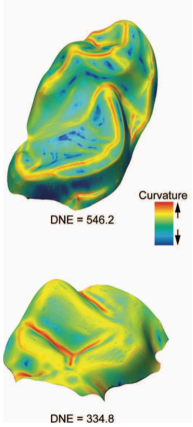


Evaluate

Ask the students to evaluate whether their hypothesized relationships matched tree you show, detailing which hypothesized relationships were supported and which were not (tree thinking challenge). Ask the students to explore in a short written passage why their hypotheses may have differed from the genetic tree in light of what they know about the way molar tooth shape responds to diet.

Extension (optional)

Explain the recently extinct subfossil lemurs of Madagascar and show this video from National Geographic describing work at an important subfossil lemur locality: **https://youtu.be/QX46qzzHGNI**. Have students formulate hypotheses as to the diets and relationships of the three subfossil lemurs in the Morphosource project (*Archaeolemur*, *Babakotia*, and *Megaladapis*) and perform independent research to see what the published scientific sources indicate about their hypotheses. Have them locate at least two peer-reviewed scientific publications, one investigating the diets of the extinct lemurs and one investigating their relationships. Final products may include written reports or presentations, produced either as individuals or in the groups formed for the in-class activities.

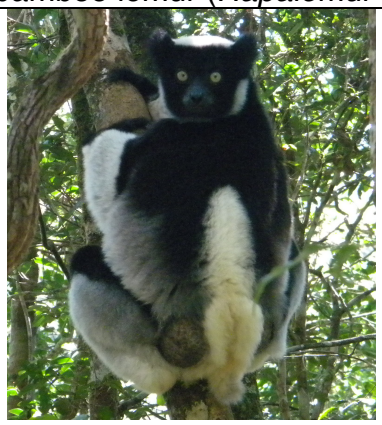


Diet from Teeth

These teeth are all lower second molars from lemur species listed below. Lemurs consume a wide variety of food resources, but most mainly rely on either leaves (*folivory*) or fruit (*frugivory*). Methods for describing the surfaces of teeth mathematically find that folivorous lemurs (left, above) have teeth with more and/or sharper cutting surfaces than lemurs that eat mostly fruit (left, below).

Which dietary pattern would you expect for each of the lemurs below base on their tooth shape?

 Wooly lemur (*Avahi laniger*)	
 Dwarf lemur (*Cheirogaleus major*)	
 Brown lemur (*Eulemur fulvus*)	

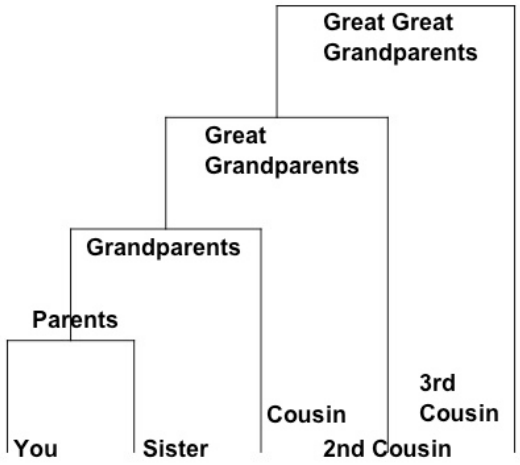
 Lesser bamboo lemur (*Hapalemur griseus*)	
 Indri (*Indri indri*)	
 Ring-tailed lemur (*Lemur catta*)	

 Sportive lemur (*Lepilemur sp.*)	
 Mouse lemur (*Microcebus murinus*)	
 Greater bamboo lemur (*Prolemur simus*)	

 Ruffed lemur (*Varecia variegata*)	

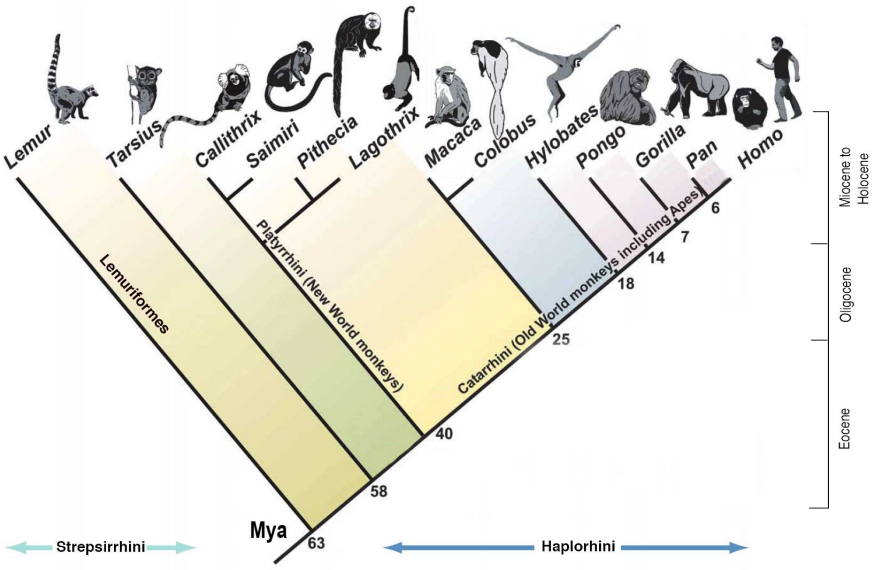
Reading Phylogenetic Trees

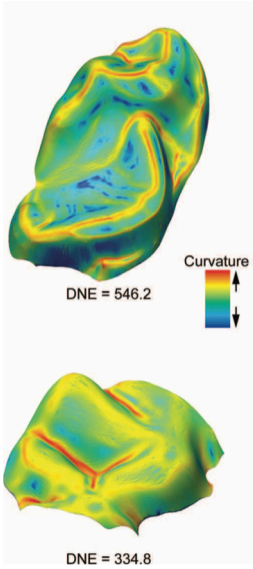
Scientists represent evolutionary relationships using a kind of graph known as a *phylogeny*. There are rules for reading phylogenies that aren't always obvious. Phylogenies represent nested relationships, with more closely related taxa sharing more ancestors than less closely related taxa. This is similar in concept to a family tree or pedigree, but in a phylogeny we care less about the identity of the ancestors themselves. A phylogenetic tree of your family might look something like this:



Notice that your sister is more closely related to you than to your first cousin, even though it might look like she's "next" to both. This is because she shares an additional pair of ancestors (your parents) with you that she doesn't with your shared first cousin. It's a *nested series*.

Below is a phylogeny of primates. It is drawn in a slightly different style but encodes the same information. Notice that humans and lemurs are relatively distantly related, last sharing a common ancestor more than 60 million years ago.



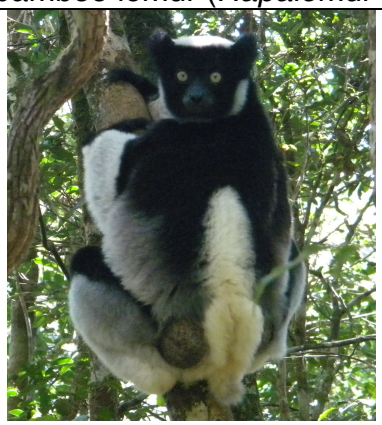


Diet from Teeth - Key

These teeth are all lower second molars from lemur species listed below. Lemurs consume a wide variety of food resources, but most mainly rely on either leaves (*folivory*) or fruit (*frugivory*). Methods for describing the surfaces of teeth mathematically find that folivorous lemurs (above, left) have teeth with more and/or sharper cutting surfaces than lemurs that eat mostly fruit (below, left).

Which would you expect for each of the lemurs below from their tooth shape?

 Wooly lemur (*Avahi laniger*)	Folivory
 Dwarf lemur (*Cheirogaleus major*)	Frugivory

 Brown lemur (*Eulemur fulvus*)	Frugivory
 Lesser bamboo lemur (*Hapalemur griseus*)	Folivory
 Indri (*Indri indri*)	Folivory
 Ring-tailed lemur (*Lemur catta*)	Frugivory (but eats lots of leaves)

 Sportive lemur (*Lepilemur sp.*)	Folivory
 Mouse lemur (*Microcebus murinus*)	Frugivory (but also eats insects, which structurally resemble leaves)
 Greater bamboo lemur (*Prolemur simus*)	Folivory

 Ruffed lemur (*Varecia variegata*)	Frugivory