FEATURE ARTICLE

Bridging Darwin's Origin of Species & Wegener's Origin of Continents and Oceans: Using Biogeography, Phylogeny, Geology & Interactive Learning

CRISTINA SOUSA

Abstract

The common ancestor and evolution by natural selection, concepts introduced by Charles Darwin, constitute the central core of biology research and education. However, students generally struggle to understand these concepts and commonly form misconceptions about them. To help teachers select the most revelant portions of Darwin's work, I suggest some sentences from On the Origin of Species and briefly discuss their implications. I also suggest a teaching strategy that uses history of science and curriculum crosscutting concepts (cause and effect) that constitute the framework to explain the evolutionary history of ratites (flightless birds) as described by Darwin, starting in the Jurassic, with the breakup of Gondwanaland, as first described by Alfred Wegener in The Origin of Continents and Oceans.

Key Words: Evolution; tree of life; common ancestor; ratites; interactive activities; databases.

It is essential that science teachers understand the pillars of the science they are focused on, so that they can guide their students to understand how science is done. *On the Origin of Species by Means of Natural Selection* is one of the most important contributions to biology, and *The Origin of Continents and Oceans* is considered the pioneer work that was fundamental for establishing the current theory of plate tectonics. The authors of these books, Charles Darwin (1809–1882) and Alfred Wegener (1880–1930), are considered the "fathers" of life sciences and earth sciences, respectively. Their theories are referred to as "revolutionary" because they promoted the fall of "fixism" – the idea that species and the positions of continents do not change over time – and the rise of evolution and mobilism in their respective fields.

Here, I describe my experience using these two episodes in the history of science in an integrated inquiry approach, focusing on aspects of the history and nature of science. My goal was to (1) encourage the development of scientific literacy in secondary and postsecondary students and (2) help students put their ideas in context and develop an integrated view of evolution and geological mobilism. I describe a novel teaching strategy that involves students in hands-on, minds-on interactive activities guided by a WebQuest (http://webquest.org). Students use cutting-edge research databases to work collaboratively and think critically about the evolutionary history of some species of ratites (flightless birds) described by Darwin.

Darwin's Theory of Evolution by Natural Selection

The theory of evolution is considered a central organizing theory for both research and education because it constitutes a generalized explanation of biological phenomena (Kiser, 2014). Therefore, one can find a growing body of literature on different strategies for teaching evolution in high school, including experimental activities (Green et al., 2011; Ratcliff et al., 2014), role-playing activities (Riechert et al., 2011), computer-simulation activities (Abraham et al., 2012; Wei et al., 2012), and problem-based learning (Sousa, 2013, 2014).

In the activities described below, I ask students to hypothesize about the mechanisms whereby geological mobilism has shaped the biodiversity and evolution of Palaeognathae (or "paleognaths"), a superorder that includes birds with a paleognathous bony palate. This superorder constitutes a monophyletic clade that contains at least 12 genera of ratites (flightless birds) and 9 genera of tinamous (short-distance and high-speed flying birds), but the phylogenetic relationships among them are still controversial. Paleognaths diverged from all the other birds (neognaths) about 131 mya (Haddrath & Baker, 2012) and include the ostrich from Africa (currently not present in Eurasia, probably due to extinction); rheas from South America; tinamous from Central and South America; emu and cassowary from Australia; kiwi from New Zealand; and two extinct species of large flightless birds, the moa of New Zealand and the elephant bird of Madagascar (Figure 1).

The world distribution of this clade – with at least one species on each continent of the Southern Hemisphere, except Antarctica – was noticed by Charles Darwin, who hypothesized that their flightless

The American Biology Teacher, Vol. 78, No 1, pages. 24–33, ISSN 0002-7685, electronic ISSN 1938-4211. ©2016 by the Regents of the University of California. All rights reserved. Please direct all requests for permission to photocopy or reproduce article content through the University of California Press's Reprints and Permissions web page, www.ucpress.edu/journals.php?p=reprints. DOI: 10.1525/abt.2016.78.1.24.



Figure 1. World distributions of native populations of paleognaths (ratites and tinamous) in the Quaternary: lesser rhea (1), greater rhea (2), tinamou (3), ostrich (4), cassowary (5), emu (7), and kiwi (8). Also included are past distributions of the recently extinct species of moa (6) and elephant bird (9). Adapted from Naish (2014).

condition was due to wing reduction over time, resulting from lack of use. He predicted that ratites were related to each other. However, there was no convincing scientific explanation for the possible mechanisms responsible for the relatedness of these flightless birds, which were found separated by thousands of kilometers of ocean, until the acceptance of continental drift and plate tectonics.

○ Continental Drift & Plate Tectonics

Continental drift was hypothesized by Alfred Wegener, mainly in his book *Die Entstehung der Kontinente und Ozeane* [*The Origin of Continents and Oceans*], first published in 1915 (we are now in its centennial). However, in 1910, similar ideas were proposed independently by Frank Taylor (1860–1938), so it is frequently referred to as the "Taylor-Wegener" theory. Wegener's book is considered a huge contribution to the acceptance of the theory of plate tectonics. First proposed by J. Tuzo Wilson, plate tectonics is the currently accepted theory that integrates the theory of continental drift and explains that all landmasses were once joined together and formed a supercontinent known as Pangaea. This provides our framework for explaining ratites' evolutionary history.

Wegener's original reconstructions of the map of the world (Figure 2) during the existence of Pangaea and upon breakup of this supercontinent illustrate his theory of horizontal displacement of continents (generally known as the "theory of continental drift"), a view opposite that of the the majority of his contemporaries. This controversy of "mobilists" and "fixists" continued for decades, until the establishment of plate tectonics theory during the 1960s (Frankel, 2012).

This teaching strategy constitutes a timely example that promotes the devolopment of students' skills related to "how science



Figure 2. Reconstruction of the map of the world according to the continental drift theory for three time points, with brief description of geological events (from left to right): Pangaea during Upper Carboniferous, ~300 mya, surrounded by one ocean known as Panthalassa; Pangaea and Gondwana fragmentation during Eocene, ~50 mya; and last steps of Gondwana separation during Lower Quaternary, ~2 mya. Maps from Wegener (1915).

is done" (San Román, 2012), using some of Wegener's sentences, such as this:

Scientists still do not appear to understand sufficiently that all earth sciences must contribute evidence towards unveiling the state of our planet in earlier times, and that the truth of the matter can only be reached by combining all this evidence.... At a specific time the earth can have had just one configuration. But the earth supplies no direct information about this.... It is only by combining the information furnished by all the earth sciences that we can hope to determine the "truth" here, that is to say, to find the picture that sets out all the known facts in the best arrangement and that therefore has the highest degree of probability. (Wegener, 1915)

Therefore, this strategy bridges life science teaching and earth science teaching through a crosscutting concept of cause-and-effect, as proposed by NGSS Lead States (2013) and the National Research Council (2012). This is accomplished by promoting students' reflection on the correlation of plate tectonics with changes in biodiversity and evolution, within the core idea LS4 "Biological Evolution: Unity and Diversity" of the *Next Generation Science Standards*. Moreover, both these episodes in the history of science are recommended examples for teaching aspects of the nature of science to high school students (NGSS Lead States, 2013).

O Bridging Paleognaths Described by Darwin & Recent Phylogenetic Evidence

Several alternative hypotheses for the phylogeny of ratites are being debated by different groups of scientists. I recommend that teachers initially engage students by having them watch *Darwin's Lost Voyage* (National Geographic, 2009). This video acquaints students with some parts of *On the Origin of Species* as well as with the socioscientific context of Darwin's life and work.

In this exercise, students examine three species described by Darwin: the ostrich (*Struthio camelus*) and two sister species in the genus *Rhea*, the common rhea (*R. americana*) and Darwin's rhea (*R. pennata*, described in 1837 as *R. darwinii*). Students examine descriptions of ratite species (from chapters XI and XII on geographic distribution), such as:

[T]he naturalist in travelling, for instance, from north to south never fails to be struck by the manner in which successive groups of beings, specifically distinct, yet clearly related, replace each other. . . . The plains near the Straits of Magellan are inhabited by one species of Rhea (American ostrich), and northward the plains of La Plata by another species of the same genus; and not by a true ostrich or emeu [sic], like those found in Africa and Australia under the same latitude. (Darwin, 1859)

Thomas Huxley, a contemporary and friend of Darwin's, described a common anatomical characteristic of ratites: the arrangement of palatal bones (in the roofs of their mouths), which Huxley considered to be more reptile-like than like that of other birds (Naish, 2014). This unique arrangement of palatal bones constitutes the diagnostic characteristic of the superorder Palaeognathae, which includes ratites (nonflying birds) and tinamous (short-distance flying birds).

Relationships among paleognaths are still controversial, and different authors present different phylogenetic trees, some showing ratites as a monophyletic group (Harshman & Brown, 2010) whereas others suggest ratite paraphyly (with moa closer to tinamous than to any other ratite; Phillips et al., 2010). Recently, new molecular techniques used to examine evolutionary relationships have confirmed the anatomy-based arguments of relatedness; however, molecular approaches are associated with some uncertainties, such as nonpreservation of fossils, which underestimates the antiquity of lineages; and calibration uncertainty, which can bias molecular divergence dating (Lee et al., 2014a).

Molecular-dating evidence places the appearance of modern birds at only 20 million years after Archaeopteryx (~150 mya), which implies that early avian evolution occurred extraordinarily rapidly (Lee et al., 2014a). Recent studies have also described the theropod lineage directly ancestral to birds, which underwent sustained miniaturization during 50 million years, evolving skeletal adaptations four times faster than other dinosaurs (Lee et al., 2014b).

One can hypothesize that the explanation for the similarities described between ratite species is the existence of a common ancestral species, one of the most important concepts proposed by Darwin (1837). Darwin was also a pioneer in introducing the tree of life (ToL) as a model of relatedness, including the existence of a common ancestor, using a drawing to represent the idea (in chapter IV on natural selection):

The affinities of all the beings of the same class have sometimes been represented by a great tree. . . . As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feebler branch, so by generation I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever branching and beautiful ramifications. (Darwin, 1859)

Figure 3 presents a simplified phylogenetic tree (with a section of Darwin's ToL model in the background) that includes the most recent common ancestor (MRCA) of three species of ratites ("species x") and the relationships of R. pennata, R. americana, and S. camelus. Darwin's observations of similarity between the rheas and the ostrich and his hypothesis of their common ancestry have been tested by analyzing their DNA sequences, and divergence times have been estimated on the basis of these sequences. Haddrath and Baker (2012) estimated that the divergence of the lineage leading to the ostrich (node 1 on Figure 3; see Appendix Figure 8) occurred at 97 mya (within the interval 89-108 mya), corresponding to the age of the MRCA of all Palaeognathae, which is in accordance with others' findings (Jarvis et al., 2014). At ~81 mya the lineage leading to rheas was separated from all others, and the MRCA of rheas (node 2 in Figure 3 and in Appendix Figure 8) was estimated at ~4 mya (Haddrath & Baker, 2012).

O Bridging Pangaea Fragmentation & Ratites' Evolutionary History

Evolution is correlated with biodiversity, which either increases by the formation of new species, for example by natural selection upon



Figure 3. Simplified phylogenetic tree of three ratites and their most recent common ancestor ("species x"). Maps show the current geographic distribution of native populations: (a) *Rhea pennata*, (b) *R. americana* (synonym of *Pterocnemia pennata*), and (c) *Struthio camelus*. Sources: Haddrath & Baker (2012) and IUCN Red List of Threatened Species database, with partial reproduction of Darwin's (1859) illustration in the background.

vicariance, or decreases by extinction. According to Darwin (1859), in chapter XI on geographic distribution:

In considering the distribution of organic beings over the face of the globe, the first great fact which strikes us is, that neither the similarity nor the dissimilarity of the inhabitants of various regions can be accounted for by their climatal and other physical conditions. . . . A second great fact which strikes us in our general view is, that barriers of any kind, or obstacles to free migration, are related in a close and important manner to the differences between the productions of various regions.

Thus, there is evidence that geological phenomena such as supercontinent formation and fragmentation, mountain formation, and glaciation are responsible for vicariance followed by natural selection, which constitutes one of the mechanisms of evolution. Geological mobilism (Frankel, 2012) has been described as being responsible for Pangaea's fragmentation (first illustrated by Wegener, 1915; see Figure 2) and the subsequent diversification of both birds and mammals (Hedges et al., 1996; Lieberman, 2005).

The fragmentation of Pangaea was responsible for the formation of two smaller supercontinents in the Late Jurassic (~150 mya): Laurasia (in the Northern Hemisphere) and Gondwanaland (mostly in the Southern Hemisphere). Africa was the first piece of Gondwanaland to separate (Wegener, 1915; Scotese, 2002), and the African ostriches were the first clade to diverge (Harshman et al., 2008; Haddrath & Baker, 2012). Therefore, Dawkins (2004) described a flightless ratite ancestor while not denying the existence of an earlier ancestor of all the ratites that flew, given that all the ratites have vestigial wings. Others have described multiple events in which the capacity to fly was lost (Harshman et al., 2008; Phillips et al., 2010) and, consequently, described ratites as a paraphyletic (or nonmonophyletic) group and Palaeognathae as a monophyletic clade (Smith et al., 2013; Baker et al., 2014).

Biogeographic processes such as vicariance and dispersal are not mutually exclusive and may be responsible for the geographically discontinuous distribution of paleognaths, given that no proposed phylogeny can be explained entirely by the fragmentation of a widespread ancestral distribution according to the order of separation of Gondwanaland fragments (i.e., vicariance). Haddrath and Baker (2012) suggested that paleognath biogeography includes two dispersals (e.g., tinamous from Australia–New Zealand to South America and Central America) and three vicariance events.

In my case study, I hypothesized that after fragmentation of Pangaea (~150 mya) the breakup of Gondwanaland occurred (~100 Ma; Figure 3, node 1), causing the South American and African populations to be geographically isolated by continental drift (Figure 2), and thus natural selection was able to act upon them separately, causing the formation of new ratite species (Figure 2 and Appendix Figure 7), in accordance with recent evidence (Haddrath & Baker, 2012; Baker et al., 2014).

Predicting the Effect of Modern & Future Environmental Changes on Paleognaths

One can find evidence that evolution has been happening at any time point and that the environment is continously changing, as described by Darwin (1859) at the end of his book:

There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed laws of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved.

Wegener (1915) performed several positional measurements and estimated an annual drift of 30 m. Although he was correct about the existence of continuous horizontal movements, his values are, generally, two orders of magnitude too high. The assembly of a novel supercontinent is expected 50 to 200 million years in the future (Williams & Nield, 2007).

While geological changes have a great impact on the environment, human activities are causing environmental changes at a rapid rate and may lead to the extinction of some species. Extinction of some ratites, such as the elephant bird (~1000 years ago) and moa (in the 13^{th} century), has already occurred as a result of human activities such as overhunting and habitat loss due to deforestation (Allentoft et al., 2014). According to BirdLife International (2012, 2014a, b), the conservation status of *R. americana* is near threatened whereas *R. pennata* and *S. camelus* are "of least concern"; however, the populations of the latter are decreasing because of hunting for meat and for export of skins and because of egg collection. Therefore, if we intend to preserve "this view of life," several

27

actions should be taken, including monitoring and effective enforcement of restrictions on illegal domestic and international trade as well as preservation of natural habitat.

In order to predict changes in geographic distribution at the levels of individual species and of monophyletic clades (e.g., paleognaths), it is important to monitor and study the causes of geographic range expansion and contraction and their consequences for ecological and evolutionary history. Paleobiogeography, using geographic information systems (GIS) and phylogenetic analyses, is a novel research field that allows analysis of the coevolution of the Earth and its biodiversity, such as by identifying vicariance and dispersal events and then studying them through the fossil record (Stigall & Lieberman, 2006). Study of the assembly and fragmentation of Pangaea and their consequences for biodiversity is relevant to predict long-term effects of changes that may occur in the future. Therefore, students are expected to hypothesize that two consequences of plate-tectonic collision (during the assembly of a supercontinent) and subsequent sea-level rise are a decrease in speciation and a rise in the extinction rates of paleognaths (WebQuest, question 4).

• Nature of Science Integrated in On the Origin of Species & The Origin of Continents & Oceans

Reading *On the Origin of Species* constitutes an opportunity to get inside the mind of a scientist who responds to anticipated challenges to his own conclusions, which he achieved by accumulating and analyzing evidence and by corresponding with experts worldwide before publishing his work. Wegener also emphasized the importance of observations and interpretations (e.g., the idea of Pangaea), and he considered that his observations could be explained by a land connection between South America and Africa that existed until a certain time point, for which he proposed two hypotheses (Jacoby, 2012): (1) that a land bridge or a connecting

WEBQUEST INQUIRY TASKS	Databases to search
 What is the current geographic distribution of ratites? (Students should be asked to produce a map representing the current distribution of 6 species of ratites: lesser rhea, greater rhea, ostrich, cassowary, emu and kiwi) 	Encyclopedia of Life (<u>//eol.org</u>) BOLD (<u>//www.boldsystems.org</u>) The IUCN Red List of Threatened Species (<u>//www.iucnredlist.org</u>)
2) What is the conservation status of each ratite species? (Students should be asked to include a reflection on causes of extinction or threat and characterize the adaptation of populations of lesser rhea, greater rhea, ostrich, cassowary, emu, kiwi, moa and elephant bird)	The IUCN Red List of Threatened Species (//www.iucnredlist.org) Global Biodiversity Information Facility (//www.gbif.org)
 What is known about the most recent common ancestor (MRCA) of the ratites described by Darwin? Hypothesize about its geographic distribution. 	• Encyclopedia of Life (<u>//eol.org</u>) • Tree of Life web project (<u>//tolweb.org</u>) • Time Tree of Life (<u>//www.timetree.org</u>)
 Argument about the evolutionary history of the ratites described by Darwin and predict their future. 	Encyclopedia of Lite (//col.org) Tree of Life web project (//tolweb.org) Time Tree of Life (//www.timetree.org) PALEOMAP Project (//www.scotese.com/ earth.htm)
5) Hypothesize about the geological and biological mechanisms responsible for the current geographic distribution of ratites.	Tres of Life web project (//tolweb.org) Time Tree of Life (//www.timetree.org) PALEOMAP Project (//www.scotese.com/ earth.htm)



continent existed and then collapsed; or (2) that a supercontinent existed, in which a rift started widening and forming an ocean. Wegener considered that the first hypothesis contradicted the concept of isostasy and that, in his model, "the sialic blocks [referring to continents] should be capable of horizontal motion in the sima" (Wegener, 1915). Using this historical episode, teachers should guide students to the importance of argumentation based on scientific evidence (Appendix Figure 7).

Students should be able to understand the importance of discussion between peers, such as in the correspondence of Darwin with Alfred Wallace and in their collaboration in scientific publications (e.g., Darwin & Wallace, 1858), as well of communication to the general public, which was the main objective of Darwin's book. The importance of communication of results to other scientists and discussion of hypotheses can be explored by using Wegener's work, which he presented in public for the first time at a conference (Wegener, 1912) before publishing his book (Wegener, 1915). Using these episodes, teachers can promote discussion about the interactions of the socioscientific context in the acceptance of theories, and about the role of the development of technology in the amount of information available and in the accuracy of observations (e.g., geodetic measurements).

Discussion of the importance of empirical observations, hypotheses, and predictions made possible by theories is exemplified by Darwin (1859), who, upon observation of *R. americana*, *R. pennata*, and *S. camelus*, hypothesized that their flightless condition had resulted from wing reduction over time due to lack of use. His prediction that ratites were related to each other can be tested using molecular techniques. Darwin was also a pioneer in introducing the tree of life (ToL) model that showed the relatedness and existence of a common ancestor (Darwin, 1837).

O WebQuest & Assessment

Collaborative work, critical thinking, and dialogue focused on scientific argumentation can increase students' reasoning abilities and conceptual

understanding, as described by Osborne (2010), so I propose an interactive activity with appropriate scaffolding (using a WebQuest) and guidance by the teacher during classes. The WebQuest (Figure 4) was designed using an inquiry-learning model, with revelant questions that facilitate the learning process and define the steps necessary to assess the effectiveness of the learning process.

After the instructor has introduced the problem (Appendix Figure 7) to the class, students start their collaborative work during two sessions, in small groups (up to five). The instructor can ask questions to keep the discussion moving forward and to reinforce argumentation by students. Then the students work outside the classroom, using what was learned and the guidance provided by the WebQuest (and with additional consulting sessions led by the teacher for some groups), and in the next session present their work to the class. The sequence of the questions was carefully designed from simple (question 1 in Figure 4) to more complex (question 5 in Figure 4). Because some of the questions suggested to the students remain to be answered by biologists, they constitute good examples of open-ended questions.

In the present state of the art, one can use several web databases to obtain biodiversity-related data, such as the Global Biodiversity Information Facility (GBIF) and the Encyclopedia of Life (EOL). The latter is characterized by its emphasis on the development of species' page and is commonly used in research to access all the revelant data about any species of interest (Figure 5). Furthermore, EOL allows searching in other web databases, such as the Tree of Life web project, focused on phylogenetic information; the IUCN Red List of Threatened Species, which includes conservation status; and Barcode of Life Data Systems (BOLD), which is focused on DNA barcoding of each species (for further details, see Appendix Figure 7) and has helped speed the discovery and classification of species (Stoeckle & Hebert, 2008).

Another source of information suggested in the WebQuest is the PALEOMAP Project (Scotese, 2002), which presents paleomaps showing the ancient mountain ranges, shorelines, and active plate boundaries as well as future maps, designed by paleogeographic modeling, showing positions of continents in the future and the formation of the next supercontinent (Scotese, 2002).

At the end of this unit, it is expected that students will have an overall picture of the hypothesis that (1) the fragmentation of Pangaea during the Cretaceous was the trigger mechanism responsible for the diversification of both birds and mammals, due mainly to vicariance events but also to dispersal events; and (2) the Cretaceous-Tertiary extinction event constituted a huge challenge to the surviving species, which, after undergoing adaptive genetic changes, were able to occupy formerly empty ecological niches. Students should understand that these are open-ended questions that are the focus of study by several scientists, and that further analysis of constant-evolutionary-rate genes of extinct and extant species is expected to provide more accurate estimates of divergence times in the near future. Further, students should understand that reconciling both paleontological and molecular-clock evidence and uncertainties may contribute to resolve paleognath relationships. Finally, students should hypothesize that developing more accurate dating of fossils and rocks - which would, in turn, increase the accuracy of dating the breakup and fusion of landmasses - will allow us to make more accurate associations between species divergence and specific geological events, with important implications for the understanding of biogeography and the evolution of species within these groups.

Recommendations for Postsecondary Education

For questions 4 and 5 of the WebQuest (Figure 4), I recommend, for K–12 and college students, an additional comparative analysis of several recent studies, not yet included in the databases of the Tree of Life web project or in the "Time Tree of Life," which allows searches of papers published in 2010 or before. By analyzing different phylogenetic trees for paleognaths, students can gain knowledge of the current debate. Therefore, students should focus on all genera of ratites and compare several papers by identifying

Rhea americana Grey Rhea learn more about names for Overview Detail Data 101 Media **Table of Contents** OVERVIEW **Brief Summary** Distribution PHYSICAL DESCRIPTION Morphology ECOLOGY Habitat **Trophic Strategy** LIFE HISTORY AND BEHAVIOR Behavior Reproduction MOLECULAR BIOLOGY AND GENETICS Molecular Biology CONSERVATION **Conservation Status** Trends Threats Management RELEVANCE TO HUMANS AND ECOSYSTEMS Benefits WKIPEDIA RESOURCES Partner links **Biomedical terms** Nucleotide sequences LITERATURE Literature references **Biodiversity Heritage Library**

Figure 5. Encyclopedia of Life interface, which allows users to search several kinds of information about each species. *Rhea americana* is the example presented. Source: EOL, Encyclopedia of Life (2014), including photo by Lip Kee Yap (Creative Commons Attribution – ShareAlike 3.0 Unported, CC-BY-SA).

29

authors' claims, new data presented, and methods used. In summary, the articles suggested describe the ostrich as an outgroup of ratites (Haddrath & Baker, 2012; Baker et al., 2014, Lee et al., 2014b; Zhou et al., 2014) and treat ratites as either (1) a monophyletic group with a sister clade of tinamous, which is consistent with evolution from a flightless common ancestor (Lieberman, 2005); or (2) a paraphyletic group (Haddrath & Baker, 2012; Smith et al., 2013), considering tinamous within ratites and that the ancestral of ratites was a flying bird, with multiple independent losses of flight within ratites (Phillips et al., 2010). The teacher should emphasize that these studies used morphological and/or molecular data,

that molecular studies consisted of sequencing either nuclear or mitochondrial DNA, and that recent studies used high-throughput sequences from ancient DNA (aDNA, from specimens of extinct species such as the little bush moa). Other related discussion topics that I consider appropriate to bring into the classroom can be delivered through argumentation- and discussion-based activities (see activities 1 and 2, below).

Postsecondary Activity 1: What Data Should Be Used to Construct a Phylogenetic Tree?

This is an argumentation activity on fossils versus molecular clocks, using scientific papers such as Hedges et al. (1996) and Yoder (2013). The teacher can initiate this discussion by describing that the fossil record of both birds and mammals is prone to a large bias in the divergence times estimated, because of the long time span between the earliest fossils (150 mya and 220 mya, respectively) and the first appearance of modern order members (65 mya), as suggested by Hedges et al. (1996). Furthermore, students should be able to discuss the advantages, disavantages, and level of uncertainty of the different methods and of the strategies of combining methods such as

- use of fossil divergence time between the ancestrors of birds and mammals as an external calibration point (Hedges et al., 1996);
- use of molecular data for inferring divergence times (Yoder, 2013);
- estimation of rates of evolution in changes/nucleotide site/million years (Beck & Lee, 2014); and
- combining paleontological evidence with morphological and molecular clocks for estimation of divergence times (dos Reis et al., 2014).

Postsecondary Activity 2: Can Mammals' Geographic Distribution Be Explained by Pangaea Breakup?

Critical thinking about the work and conflicting views of two research groups – O'Leary et al. (2013a, b) and dos Reis et al. (2014) – should be performed by students as an extension activity that allows them to use their acquired knowledge on ratites as background to discuss mammals' biogeography. I suggest focusing on the timing of the root of the tree: that is, Late Jurassic–Early Cretaceous (Luo et al., 2011; Beck & Lee, 2014; dos Reis et al., 2014) versus post-Cretaceous–Paleogene mass extinction (O'Leary et al., 2013a, b). The relationships and timing of diversification (Teeling & Hedges, 2013) are currently under debate, so I propose that students discuss and focus on three main branches (Figure 6),



Figure 6. Two of the competing hypotheses of mammalian rooting (Morgan et al., 2013). One hypothesis (a) is in accordance with the vicariance model and supported by molecular data (Morgan et al., 2013); the other hypothesis (b) is supported by molecular data (Romiguier et al., 2013) and paleontological studies (Bennett, 2012).

such as Monotremata, Marsupialia, and placental mammals belonging to the superorders Xenarthra and Afrotheria (Morgan et al., 2013), using the web databases in Figure 4. Then the geographic distribution and the evolutionary history of these mammals should be studied by using databases proposed in the WebQuest (see Figure 4).

It is important that students understand that, although important studies have been performed in recent years – including paleontological and molecular evidence as well as inferred molecular clocks – mammalian evolution is complex, and there are still several competing hypotheses and a lot to learn.

○ Summary

Aspects of the nature of science, such as scientific argumentation and the influence of technological advances in scientific progress, should constitute a large part of life science classes. This can be accomplished by using relevant episodes in the history of science, such as the "revolutions" of Darwin and Wegener (Appendix Figure 8). Teachers can engage students with multimedia documents and discussion, and then students should be challenged, working in small groups and using scientific argumentation, to explore the problematic questions in the WebQuest and to infer that Gondwanaland's fragmentation is one explanation for the evolutionary history of rheas and ostrich. Thus, this teaching strategy is a timely example of bridging the life sciences and earth sciences through an integrated approach that helps students put ideas in context by using a crosscutting concept (cause and effect) that promotes their critical thinking on the role of geological mobilism in biodiversity changes and evolution.

O Acknowledgments

I thank the anonymous reviewers for useful comments and suggestions. I thank Faculdade de Ciências, Universidade do Porto, Portugal, for financial support. Special thanks to my students for participating in the activities and to all who have inspired and encouraged me.

References

Abraham, J.K., Perez, K.E., Downey, N., Herron, J.C. & Meir, E. (2012). Short lesson plan associated with increased acceptance of evolutionary theory and potential change in three alternate conceptions of macroevolution in undergraduate students. *CBE Life Sciences Education, 11*, 152–164. Allentoft, M.E., Heller, R., Oskam, C.L., Lorenzen, E.D., Hale, M.L., Gilbert, M.T.P. et al. (2014). Extinct New Zealand megafauna were not in decline before human colonization. *Proceedings of the National Academy of Sciences* USA, 111, 4922–4927.

Baker, A.J., Haddrath, O., McPherson, J.D. & Cloutier, A. (2014). Genomic support for a moa-tinamou clade and adaptive morphological convergence in flightless ratites. *Molecular Biology and Evolution*, 31, 1686–1696.

Beck, R.M.D. & Lee, M.S.Y. (2014). Ancient dates or accelerated rates? Morphological clocks and the antiquity of placental mammals. Proceedings of the Royal Society of London Series B, 281, 20141278.

Bennett, V. (2012). Fossil focus: marsupial evolution – a limited story? Palaeontology Online, 2(10), 1–9.

BirdLife International (2012). Rhea americana. IUCN Red List of Threatened Species. Version 2014.2. Available online at http://www.iucnredlist.org/ details/22678073/0.

BirdLife International (2014a). Rhea pennata. IUCN Red List of Threatened Species. Version 2014.2. Available online at http://www.iucnredlist.org/ details/22728199/0.

BirdLife International (2014b). *Struthio camelus*. IUCN Red List of Threatened Species, version 2014.2. Available online at http://www. iucnredlist.org/details/45020636/0.

Darwin, C. (1859). On the Origin of Species. [Reprint edition, 1985. London, UK: Penguin Classics.]

Darwin, C. (1837–1868). Notebook B: transmutation. Available online at http://darwin-online.org.uk/content/frameset?itemID=CUL-DAR121.-&viewtype=side&pageseq=1.

Darwin, C. & Wallace, A. (1858). On the tendency of species to form varieties; and on the perpetuation of species by natural means of selection. *Journal of the Proceedings of the Linnean Society of London* (*Zoology*), 3, 45–50. Available online at http://darwin-online.org.uk/ content/frameset?itemID=F350&viewtype=text&pageseq=1.

Dawkins, R. (2004). The Ancestor's Tale: A Pilgrimage to the Dawn of Evolution. Boston, MA: Houghton Mifflin.

dos Reis, M., Donoghue, P.C.J. & Yang, Z. (2014). Neither phylogenomic nor palaeontological data support a Palaeogene origin of placental mammals. *Biology Letters*, 10, 20131003. Available online at http://dx. doi.org/10.1098/rsbl.2013.1003.

EOL, Encyclopedia of Life (2014). *Rhea americana*. Available online at http://eol.org/pages/1178370/details.

Frankel, H.R. (2012). How the mobilism debate was structured. In *The Continental Drift Controversy, vol. 1.* Cambridge, UK: Cambridge University Press.

Green, J.H., Koza, A., Moshynets, O., Pajor, R., Ritchie, M.R. & Spiers, A.J. (2011). Evolution in a test tube: rise of the Wrinkly Spreaders. *Journal of Biological Education*, 45, 54–59.

Haddrath, O. & Baker, A.J. (2012). Multiple nuclear genes and retroposons support vicariance and dispersal of the palaeognaths, and an Early Cretaceous origin of modern birds. *Proceedings of the Royal Society of London Series B, 279*, 4617–4625.

Harshman, J., Braun, E.L., Braun, M.J., Huddleston, C.J., Bowie, R.C.K., Chojnowski, J.L. et al. (2008). Phylogenomic evidence for multiple losses of flight in ratite birds. *Proceedings of the National Academy of Sciences USA*, 105, 13462–13467.

Harshman, J. & Brown, J.W. (2010). Palaeognathae. Version 13 May 2010 (under construction). Tree of Life web project. Available online at http://tolweb.org/Palaeognathae/15837/2010.05.13.

Hedges, S.B., Parker, P.H., Sibley, C.G. & Kumar, S. (1996). Continental breakup and the ordinal diversification of birds and mammals. *Nature*, *381*, 226–229.

Jacoby, W.R. (2012). Alfred Wegener - 100 years of mobilism. *Geoscientist*, 22, 12-17.

Jarvis, E.D., Mirarab, S., Aberer, A.J., Bo, L., Houde, P., Li, C. et al. (2014). Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science*, *346*, 1320–1331. Kiser, S. (2014). The importance of teaching evolution. *American Biology Teacher*, *76*, 72–73.

Lee, M.S.Y., Cau, A., Naish, D. & Dyke, G.J. (2014a). Morphological clocks in paleontology, and a Mid-Cretaceous origin of crown Aves. Systematic Biology, 63, 442–449.

Lee, M.S.Y., Cau, A., Naish, D. & Dyke, G.J. (2014b). Sustained miniaturization and anatomical innovation in the dinosaurian ancestors of birds. *Science*, 345, 562–566.

Lieberman, B.S. (2005). Geobiology and paleobiogeography: tracking the coevolution of the Earth and its biota. Palaeogeography, Palaeoclimatology, Palaeoecology, 219(1-2), 23-33.

Luo, Z.-X., Yuan, C.-X., Meng, Q.-J. & Ji, Q. (2011). A Jurassic eutherian mammal and divergence of marsupials and placentals. *Nature*, 476, 442–445.

Morgan, C.C., Foster, P.G., Webb, A., Pisani, D., McInerney, J. & O'Connell, M.J. (2013). Heterogeneous models place the root of the placental mammal phylogeny. *Molecular Biology and Evolution*, 30, 2145–2156.

Naish, D. (2014). Controversies from the world of ratite and tinamou evolution (part I). Scientific American blog. Available online at http:// blogs.scientificamerican.com/tetrapod-zoology/2014/03/18/ratites-andtinamous-part-i/.

National Geographic (2009). Darwin's Lost Voyage. [Film.] Washington, DC: National Geographic Society.

National Research Council (2012). A Framework for K-12 Science Education: Practices, Crosscutting Concepts, and Core Ideas. Washington, DC: National Academies Press.

NGSS Lead States (2013). Next Generation Science Standards: For States, By States [APPENDIX H. Understanding the Scientific Enterprise: The Nature of Science in the Next Generation Science Standards]. Washington, DC: National Academies Press. Available online at http:// www.nextgenscience.org/next-generation-science-standards.

O'Leary, M.A., Bloch, J.I., Flynn, J.J., Gaudin, T.J., Giallombardo, A., Giannini, N.P. et al. (2013a). The placental mammal ancestor and the post–K-Pg radiation of placentals. *Science*, 339, 662–667.

O'Leary, M.A., Bloch, J.I., Flynn, J.J., Gaudin, T.J., Giallombardo, A., Giannini, N.P. et al. (2013b). Response to comment on "The placental mammal ancestor and the post-K-Pg radiation of placentals." *Science*, 341, 613.

Osborne, J. (2010). Arguing to learn in science: the role of collaborative, critical discourse. *Science*, *328*, 463–466.

Phillips, M.J., Gibb, G.C., Crimp, E.A. & Penny, D. (2010). Tinamous and moa flock together: mitochondrial genome sequence analysis reveals independent losses of flight among ratites. *Systematic Biology*, 59, 90–107.

Ratcliff, W.C., Raney, A., Westreich, S. & Cotner, S. (2014). A novel laboratory activity for teaching about the evolution of multicellularity. *American Biology Teacher*, *76*, 81–87.

Riechert, S.E., Leander, R.N. & Lenhart, S.M. (2011). A role-playing exercise that demonstrates the process of evolution by natural selection: caching squirrels in a world of pilferers. *American Biology Teacher*, 73, 208–212.

Romiguier, J., Ranwez, V., Delsuc, F., Galtier, N. & Douzery, E.J. (2013). Less is more in mammalian phylogenomics: AT-rich genes minimize tree conflicts and unravel the root of placental mammals. *Molecular Biology* and Evolution, 30, 2134–2144.

San Román, L.S. (2012). Aniversarios en ciencias: algunas orientaciones para su uso didáctico [Anniversaries in Sciences: some orientations for teaching use]. *Enseñanza de las Ciencias de la Tierra, 20*, 96–104.

Scotese, C.R. (2002). Atlas of Earth History, vol. 1: Paleogeography. Arlington, TX: PALEOMAP Project. Available online at http://www. scotese.com.

Smith, J.V., Braun, E.L. & Kimball, R.T. (2013). Ratite nonmonophyly: independent evidence from 40 novel loci. Systematic Biology, 62, 35–49.

Sousa, C. (2013). Implementation of problem-based learning in the context of celebrating the centenary of Alfred Wegener's first publication on continental drift and bridging the evolution science – biology and geology teaching practice gap. In Abstract Book of Congress of the European Society for Evolutionary Biology (p. 1081). Lisboa, Portugal.

- Sousa, C. (2014). History and nature of science enriched problem-based learning on the origins of biodiversity and of continents and oceans. *Multidisciplinary Journal for Education, Social and Technological Sciences*, 1, 142–159.
- Springer, M.S., Meredith, R.W., Teeling, E.C. & Murphy, W.J. (2013). Technical comment on "The placental mammal ancestor and the post-K-Pg radiation of placentals." *Science*, 341, 613.
- Stigall, A.L. & Lieberman, B.S. (2006). Quantitative palaeobiogeography: GIS, phylogenetic biogeographical analysis, and conservation insights. *Journal of Biogeography*, 33, 2051–2060.
- Stoeckle, M.Y. & Hebert, P.D.N. (2008). Barcode of life. *Scientific American* (October), 82-88.
- Teeling, E.C. & Hedges, S.B. (2013). Making the impossible possible: rooting the tree of placental mammals. *Molecular Biology and Evolution*, *30*, 1999–2000.
- Wegener, A.L. (1912). Die Entstehung der Kontinente. Geologische Rundschau, 3, 276–292.

- Wegener, A.L. (1915). *Die Entstehung der Kontinente und Ozeane* [The Origin of Continents and Oceans]. Braunschweig, Germany: Friedrich Vieweg & Sohn.
- Wei, C.A., Beardsley, P.M. & Labov, J.B. (2012). Evolution education across the life sciences: making biology education make sense. CBE Life Sciences Education, 11, 10–16.
- Williams, C. & Nield, T. (2007). Pangaea, the comeback. *New Scientist* (17 October), 37-40.
- Yoder, A.D. (2013). Fossils versus clocks. Science, 339, 656-658.
- Zhou, Q., Zhang, J., Bachtrog, D., An, N., Huang, Q., Jarvis, E.D. et al. (2014). Complex evolutionary trajectories of sex chromosomes across bird taxa. *Science*, 346, 1332.

CRISTINA SOUSA was a Research Fellow at Massachusetts General Hospital and Harvard Medical School and presently works as a teacher and researcher at Faculdade de Ciências, Universidade do Porto, Portugal. E-mail: up199502480@fc.up.pt.

BIODIVERSITY AND DNA BARCODING

DNA barcoding constitutes a novel tool for taxonomists, as well as an innovative device for quick identification. The gene region used as the barcode for almost all animal groups is a standard portion of the mitochondrial cytochrome c oxidase 1 gene (CO1), while for plants there are two gene regions in the chloroplast, matK and rbcL, that are used as barcode. Portion of the barcode of two wild specimens (*Rhea pennata* and *Rhea americana*) and one extinct, museum and voucher specimen (*Dinornis giganteus*) are presented below.



Figure - Selected portion of the barcodes (nucleotide 776 to 806) of *Rhea pennata* (BOLD:AAF7583), *Rhea americana* (BOLD:AAD5945) and *Dinornis giganteus* (BOLD:AAX9559). Each bar corresponds to one nucleotide position of CO1 gene, usually represented in colours, such as each color represents one nucleotide A (green), T (red), C (blue) and G (black). Source: BOLD.

BOLD database constitutes the permanent public repository for barcode data records (recording biodiversity) allowing researchers to assemble their data on wild, commercial, and voucher (or museum) specimens.

Appendix Figure 7. Supporting material: biodiversity and barcoding.



To what extent has geologic mobilism impacted the evolution of ratites?

"The first concept of continental drift first came to me as far back as 1910, when considering the map of the world, under the direct impression produced by the congruence of the coastlines on either side of the Atlantic." (Wegener, 1915)

"In my model the sialic blocks should be capable of horizontal motion in the sima." "(...) continent cannot sink, for it is lighter than that upon which it is floating. Therefore, let us, just for once, take [displacement] into consideration!" (Wegener, 1912)



"Scientists still do not appear to understand sufficiently that all earth sciences must contribute evidence towards unveiling the state of our planet in earlier times, and that the truth of the matter can only be reached by combining all this evidence. (...) At a specific time the earth can have had just one configuration. But the earth supplies no direct information about this. We are like a judge confronted by a defendent who declines to answer, and we must determine the truth from the circumstantial evidence. (...) How would we assess a judge who based his decision on part of the available data only?

(1915) It is only by combining the information furnished by all the earth sciences that we can hope to determine the "truth" here, that is to say, to find the picture that sets out all the known facts in the best arrangement and that therefore has the highest degree of probability." (Wegener, 1915)

In what way does the evidences presented by Wegener support his theory of continental drift? What additional evidence was gathered and integrated into plate tectonics?



Charles Darwin and Alfred Wegener have something in common: they both faced fixist opponents. In 1859, Darwin presented in "On the Origin of Species" his view of changes through time in the number and characteristics of the species found in one place by natural selection;

Wegener in "The Origins of Continents and Oceans" proposes that the geographic position of continents has changed by horizontal displacement (or continental drift).

What are the mechanisms responsible for the geographic distribution of several ratites?

Darwin (1859) described two species, similar to the African ostrich, that were found in different regions of South America. In 1841 the lesser rhea

was named Rhea darwinii.



Recent phylogenetic studies show the distribution of these species of rheas (tree of Paleognathae, on the right).

11850

How can one explain the presence of a certain species in one place and its absence in another, with similar climates?
Source: Baker et al. (2014), Darwin (1937), Nalsch (2014), Wegener (1915).



Appendix Figure 8. The problem: To what extent has geologic mobilism influenced the evolution of ratites?

33

Thank You NABT Sustaining Members!

PLATINUM LEVEL SUSTAINING MEMBERS

Bio-Rad Laboratories www.bio-rad.com

> Froguts, Inc. www.froguts.com

Carolina Biological Supply Company www.carolina.com

Howard Hughes Medical Institute www.hhmi.org

Macmillian New Ventures www.macmillannewventures.com

> Pearson Education www.pearsoned.com

Vernier Software & Technology www.vernier.com

GOLD LEVEL SUSTAINING MEMBERS:

Seaworld Parks & Entertainment seaworldparks.com/teachers

SILVER LEVEL SUSTAINING MEMBERS

BSCS

www.bscs.org

BRONZE LEVEL SUSTAINING MEMBERS

Happy Teachers www.happyteachers.net

> PASCO Scientific www.pasco.com

Sustaining Members share NABT's mission to promote biology and life science education. Call NABT at (888) 501-NABT or visit www.NABT.org to learn more.