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Darwin's two competing phylogenetic trees: marsupials as ancestors or sister taxa?

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ABSTRACT: Studies of the origin and diversification of major groups of plants and animals are contentious topics in current evolutionary biology. This includes the study of the timing and relationships of the two major clades of extant mammals - marsupials and placentals. Molecular studies concerned with marsupial and placental origin and diversification can be at odds with the fossil record. Such studies are, however, not a recent phenomenon. Over 150 years ago Charles Darwin weighed two alternative views on the origin of marsupials and placentals. Less than a year after the publication of On the origin of species, Darwin outlined these in a letter to Charles Lyell dated 23 September 1860. The letter concluded with two competing phylogenetic diagrams. One showed marsupials as ancestral to both living marsupials and placentals, whereas the other showed a non-marsupial, non-placental as being ancestral to both living marsupials and placentals. These two diagrams are published here for the first time. These are the only such competing phylogenetic diagrams that Darwin is known to have produced. In addition to examining the question of mammalian origins in this letter and in other manuscript notes discussed here, Darwin confronted the broader issue as to whether major groups of animals had a single origin (monophyly) or were the result of "continuous creation" as advocated for some groups by Richard Owen. Charles Lyell had held similar views to those of Owen, but it is clear from correspondence with Darwin that he was beginning to accept the idea of monophyly of major groups.

KEY WORDS : homology - T. H. Huxley - C. Lyell - monophyly - R. Owen - G. R. Waterhouse.

INTRODUCTION

Questions concerning the origin and diversification of major clades of both plants and animals are far-reaching and contentious topics in evolutionary biology. Along with the so-called Cambrian explosion of animals with hard parts, the timing of the origin and diversification of major clades of therian mammals (metatherians and eutherians) are some of the most keenly debated evolutionary events. Molecular systematics have played an increasingly central role in elucidating the relationships of extant mammal species and in the arguments for the timing of their origin and diversification (Murphy *et al.* 2001, 2003; Bininda-Emonds *et al.* 2007; Meredith *et al.* 2011). In some cases the age estimates of these events based on molecules and fossils are at considerable odds (Wible *et al.* 2007). Luo and colleagues (2011) have described what they claim is the earliest eutherian mammal (the clade including extant placentals) from China from 160 million-year old rocks, although this may prove to be a species predating the split between metatherians and eutherians. If this does prove to be a eutherian, it would accord better with dates of around 150 million years based on some molecular studies (Archibald 2011), but even more recent molecular dates

suggest 190 million years for the split between metatherians (including marsupials) and eutherians (including placentals) (Meredith *et al.* 2011).

The study of marsupial and placental diversification, however, is not simply a recent concern. Over 150 years ago Charles Darwin contemplated how marsupials and placentals originated. These ruminations are found in two diagrams, labelled "Diagram I." and "Diagram II" which accompanied a letter that Darwin wrote to Charles Lyell on 23 September 1860¹ (Burkhardt *et al.* 1993), less than a year after the publication of *On the origin of species*. Discussions of this letter, his two diagrams, and changing views of higher relationships of mammals are the subjects of this paper, as well as Darwin's confrontation of the monophyly of various groups. It should be noted that monophyly is now more precisely used to define a group that includes all (known) descendant species and their most recent common ancestor. It was used less precisely in Darwin's time to include what we now term paraphyletic groups. For example, Reptilia excluding birds would have been deemed monophyletic in Darwin's day by most biologists, but is deemed paraphyletic in today's usage.

Over much of his adult life Darwin produced relatively few tree-like diagrams showing both his view of how evolution operated (process) and his view of how evolution manifested itself (pattern). Further, of this number, the only one that was unquestionably for public consumption was the single figure in *On the origin of species*, a foldout (Darwin 1859: between 116 and 117), showing how he perceived evolution to operate. Given what today we might call his preoccupation with evolution, this seems a paltry number of such trees. Many of Darwin's other tree-like diagrams, now widely available in print and online, were either in private notes, in letters to colleagues, or were intended for publications that never saw the light of day in his lifetime, including his two mammal phylogeny diagrams, which he sent to Lyell in September 1860. As far as I can determine, these are the only phylogenies about which Darwin offered two alternate views of evolutionary history.

DARWIN'S MAMMALIAN PHYLOGENETIC TREES

I am aware of five of Darwin's tree diagrams dealing with various mammals that he did not publish. Beginning with the best-known and phylogenetically most specific tree, Darwin produced a diagram in one of his notebooks in 1868 dealing with primate evolutionary relationships² (Figure 1; see also Voss 2010).

A lesser-known diagram of uncertain date, but probably the 1840s or 1850s, dealt with the broader question of rodent and marsupial evolution³ (Figure 2). Voss (2010: figure 30 and plate 6) presented this diagram, commenting only that it showed the history of rodents or marsupials. It is annotated at the top, "Let dots represent Genera ???". Below this, to the right, Darwin wrote "no form intermediate". A pencil line leads to the largest dot at the base of the tree or possibly to the dotted lines below, thus "no form intermediate" almost certainly refers to the lack of species intermediate between marsupials and placentals (possibly more specifically rodents). The text on the left probably reads "If these had all given descendants then this wd [would] have been a great series", and a line leads to an encircled group of five dots near the base of the tree. He was indicating that this cluster of dots did not radiate into many other species, but would have been significant if they had done so. At the very base of the tree Darwin wrote "Parent of Marsupials & Placentals" with

the word "Rodents" written over the main middle trunk of the tree. Here are two groups that did very successfully radiate as indicated by many connected dots. To the right, partial circles enclose the tree. Short lines labelled "Rodents" and "Marsupials" point to the middle and lower main trunks, respectively. Voss (2010: figure 29) published another drawing by Darwin using the same branching motif with dots for "new forms" as well as similar concentric circles labelled for geological intervals.

Voss (2010: 108) noted that this motif is derived from a similar drawing by Louis Agassiz. As she indicated that, unlike Agassiz, Darwin connected the dots in his tree to form a phylogeny. In his 1844 tree-like diagram of fish Agassiz intentionally had not connected the various lineages (Archibald 2009), about which he wrote (Agassiz 1844: 170),

Finally the convergence of all these vertical lines indicates the affinity of families with the principal stock of each kind. I however did not bind the side branches to the principal trunks because I have the conviction that they do not descend the ones from the others by way of direct procreation or successive transformation, but that they are materially independent one from the other, though forming integral part of a systematic unit, whose connection can be sought only in the creative intelligence of its author.

It at first may seem odd that Darwin should juxtapose rodents and marsupials in such a tree. Based on discussions and correspondence with G. R. Waterhouse, there was some idea of a possible relationship between rodents and marsupials (Darwin 1859: 430). This idea is reinforced in another, simpler diagram⁴ also probably from the 1840s or 1850s that was labelled "Parents of Placentals Rodents & Marsupials" (Figure 3). The probable relevance of rodents and marsupials in both of these trees is discussed later.

The fourth and fifth trees, which are the subject of this paper, lay out two schemes for the origin of the two great clades of living therian mammals, marsupials and placentals. Although edited versions of these diagrams have been published in at least two sources (Darwin 1887: 343; Burkhardt *et al.* 1993: 377) to my knowledge, this is the first time that the original manuscripts have been reproduced (Figures 4 and 5; see pp 224 and 225) and their significance discussed. The two diagrams accompanied the ten-page letter from Darwin to Charles Lyell on 23 September 1860 during Darwin's vacation with his family at a seaside hotel in Eastbourne. This letter to Lyell came just 10 months after the publication of *On the origin of species*.

These five mammalian diagrams have not engendered as much interest as others of Darwin's trees such as those in his 1837–1838 notebook B (de Beer 1960); nevertheless, they offer insights into Darwin's specific views on both the process and pattern of early mammal evolution, and more generally his views on monophyly in evolutionary history. They enforce the emerging view in the middle of the nineteenth century that the history of life was more like a tree than a ladder-like progression of lower to higher forms (Archibald 2009). As noted above, as far as is known, Darwin produced no other trees showing alternative phylogenetic hypotheses.

MONOPHYLY, HOMOLOGY, CONVERGENCE, CONTINUOUS CREATION, AND SPONTANEOUS GENERATION

The first page and a half of Darwin's letter to Lyell¹ dealt with reviews of *On the origin of species*, as well as family travels, and the death of T. H. Huxley's young son. In the middle of the second page of the letter, Darwin began to discuss the issue of mammalian origins with the following passage ending at the top of the fourth page.



Figure 1. A phylogenetic tree drawn by Charles Darwin in 1868 showing specific hypotheses of relationships among various groups of primates.² (Reproduced by permission of the Syndics of Cambridge University Library.)

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Figure 2. A phylogenetic tree of mammals, drawn by Charles Darwin in the 1840s or 1850s.³ Other than showing placentals (specifically rodents) and marsupials as sister taxa, there are no other hypotheses of relationship given. (Reproduced by permission of the Syndics of Cambridge University Library.)



Figure 3. A phylogenetic tree of mammals, drawn by Charles Darwin in the 1840s or 1850s.⁴ Although placentals and marsupials are indicated, no lower level taxa are identified on the tree. (Reproduced by permission of the Syndics of Cambridge University Library.)

I quite misunderstood you on Types. I have a very decided opinion that all Mammals must have descended from a <u>single</u> parint [*sic*]. Reflect on the multitude of details, very many of them of extremely little importance to their habits (as number of bones of head &c – covering of hair, identical Embryological development &c &c): now this large amount of similarity I must look at as certainly due to inheritance from a common stock. I am aware that some cases occur in which the latter a similar or nearly similar organ, has been acquired by independent acts of nat. selection, but in most of such cases of these apparently so closely similar organs, some important homological difference may be detected. Please read p. 193 beginning "The Electric organs" & trust me that the sentence "In all these cases of two very distinct species &c &c' was not put in rashly; for I went carefully into every case. – Apply this organ argument to the whole frame, internal & external, of mammifers, & you will see why I think so strongly that all have descended from one progenitor. – I have just reread your letter & I am not perfectly sure that I understand your point.

The most relevant sentence from page 193 of On the origin of species that Darwin cited is:

Generally when the same organ appears in several members of the same class, especially if in members having very different habits of life, we may attribute its presence to inheritance from a common ancestor; and its absence in some of the members to its loss through disuse or natural selection.

He continued later on the same page:

... natural selection, working for the good of each being and taking advantage of analogous variations, has sometimes modified in very nearly the same manner two parts in two organic beings, which owe but little of their structure in common to inheritance from the same ancestor.

These sentences, as well as the passage (quoted above) from his letter to Lyell, are a clear endorsement of a single ancestry for mammals. Additionally, three other important evolutionary concepts were addressed in this paragraph – monophyly, homology, and convergence. Darwin's reference to "Types" concerned the issue of monophyly. On 18 September 1860, Lyell had written to Darwin, "You need not be afraid of my starting any theory of successive creation of types" (Burkhardt *et al.* 1993: 366). Lyell had been grappling with whether various groups had a single or multiple origins. This was no small question of the time.

DARWIN'S COMPETING PHYLOGENETIC TREES

As Cosans (2009: 97–103) has noted, the champion of "continuous creation", Richard Owen, did not so much reject species change, but rather he rejected Darwin's thesis that natural selection could have been the guiding force from a common ancestor. Owen did not believe natural selection was supported by comparative anatomy and embryology. Rather, for Owen, archetypes had been created, from which species in a group repeatedly evolved, resulting in multiple or successive origins of members of that group (Cosans 2009; Desmond 1982: 60–65), although for mammals, he appears to have supported monophyly.⁵

In the same letter Lyell wrote (Burkhardt et al. 1993: 366),

Can we assume as at all probable that all mammalia came from one original Stock instead of several distinct mammalian-types each developed by small & successive modifications out of lower ornithic reptilian or perhaps monotrematous prototypes. It would greatly simplify matters if single & exclusive areas could be assigned or even speculated upon, on some even slight data, or if single periods could be proposed as those of the first coming in of mammalia. But as I understand your views this is not very probable.

Darwin was not entirely clear, in his letter to Lyell, when he wrote that he was "not perfectly sure that I understand your point." Lyell's reply, dated 25 September 1860 (Burkhardt *et al.* 1993: 384), cleared up this matter:

I think you have understood my point & the idea that if the original type of Mammalia had been lost & the reptilian had been greatly raised in grade, they w^d. [would] have produced some other great class as high perhaps or higher but not the existing Mammalia, is a grand notion & believing as I do in the infinite Capacity of the creative power, inherent in the organic world, worked out by variation & natural selection, I do not think it an extravagant speculation at all.

Even though he had previously endorsed multiple or successive origins/creations within given groups such as mammals, Lyell here strongly endorsed Darwin's argument of the monophyly of Mammalia specifically and the likelihood for the monophyly for major groups in general.

Darwin had not always been sure of the monophyly of various groups. He had been struggling with the question of the single origin of life, dogs, and even humans. In his letter to Lyell, starting at the bottom of the seventh page, Darwin wrote:

I do not think multiple origin of dogs goes against single origin of man. ... All the races of man are so infinitely closer together than to any ape, that (as in case of descent of all mammals from one progenitor) I sh^d [should] look at all races of man as having certainly descended from single parent. ... Supposing, as I for one believe that our dogs have descended from 2 or 3 wolves, jackalls &c; yet these have, <u>on our view</u>, descended from single remote unknown progenitor. With domestic dogs the question is simply whether the whole amount of difference has been produced since man domesticated a single species; or whether part of the difference arose in the state of nature.

Darwin could not be more emphatic that all living humans share a single common human ancestor. For domestic dogs he was also arguing that they share a common ancestor, but one of more ancient status. Darwin and Lyell had for some years corresponded on the question of the ancestry of the domestic dog (Dixon and Radick 2009; van Wyhe 2011) and of other groups as well. The question for Darwin was whether all domestic dogs descended from the wolf (*Canis lupus*) or mostly wolf but with contributions from some species of jackal (*Canis spp*) or coyote (*Canis latrans*). Molecular tools have confirmed the certainty of a wolf ancestry (Vila *et al.* 1997).

Darwin was equally emphatic that mammals had a single origin, as is clear from his letter to Lyell just quoted – "mammals must have descended from a single parent", "this large amount of similarity I must look at as certainly due to inheritance from a common stock",

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Figure 4. Diagram I, a phylogenetic tree showing a non-marsupial, non-placental mammal common ancestor for marsupials and placentals¹. This is one of two (see Figure 5 for the other) hypothetical mammal phylogenies drawn by Charles Darwin to accompany his letter of 23 September 1860, sent to Charles Lyell. (Reproduced with permission of the American Philosophical Society.)





Figure 5. Diagram II, a phylogenetic tree showing a marsupial as the common ancestor for both marsupials and placentals¹. This is one of two (see Figure 4 for the other) hypothetical mammal phylogenies drawn by Charles Darwin to accompany his letter of 23 September 1860, sent to Charles Lyell. (Reproduced with permission of the American Philosophical Society.)

and "all have descended from one progenitor." His argument rested on the presence in all mammals of "multitude of details, very many of them of extremely little importance to their habits (as the number of bones of head &c – covering of hair, identical embryological development &c &c)". Darwin went on to comment about the independent acquisition of "a similar or nearly similar organ", but noted that for most of these "some important homological difference may be detected." That is, these similarities do not come from common ancestry but from similar ecological constraints.

In this passage Darwin was most probably using homology similar to that of Richard Owen (1843), who defined it as "the same organ in different animals under every variety of form and function." For Owen, his "archetype" for each major group was the source of homologies or homologues (Cosans 2009). Additionally, Owen (1860) accepted that simple forms were constantly arising from non-living matter – spontaneous generation – and simpler forms sharing an archetype were repeatedly giving rise to more complex forms – "the succession of forms throughout time and space" (Cosans 2009). In Darwin's correspondence with Lyell, the source of these homologies was common descent not Owen's archetype. Common descent or monophyly is of course the source that most biologists today attribute to homologies.

Darwin opposed Owen's ideas of a repeated succession of simple to complex forms within a given group, instead favouring monophyly for most groups. This view is quite evident in the penultimate sentence in his letter to Lyell:

If every Vertebrate were destroyed throughout the world except our <u>now well established</u> Reptiles, millions of ages might elapse before Reptiles could become highly developed on a scale equal to mammals; & on principle of inheritance they would make some quite new Class & not Mammals, – though possibly more intellectual!!

He is expressing the view that reptiles, or what we today call non-mammalian synapsids, could give rise to other groups but they would not be mammals. This is reminiscent of, but certainly not the same as, Gould's (1989) well-known argument that if rewound, evolution's tape would not produce the same forms, that is, historical contingency.

The ideas of monophyly and homology (which is used to establish monophyly) were certainly the most evolutionary germane concepts pertaining to mammal origins and origins in general in Darwin's letter to Lyell and in *On the origin of species*. Nonetheless, the ecological counterpart to monophyly/homology, which we now term convergence, was also expressed well by Darwin when he wrote of "natural selection" working on "analogous variations" to modify organisms in the same manner, but not because of common inheritance. Even today, trying to tease apart resemblances resulting from monophyly/homology versus resemblances arising from ecological convergences can be a difficult task. Darwin was clearly noting the fact that similar selective environmental pressures can result in similar anatomical solutions.

TWO MAMMAL TREES: MARSUPIALS AS ANCESTORS OR SISTER TAXA

Darwin's discussion of his two diagrams began on the fourth page of his letter to Lyell: "I enclose 2 diaggrams [*sic*] showing the sort of manner I <u>conjecture</u> mammals have been developed: I thought a little on this, when writing p. 429 beginning "Mr. Waterhouse". – (please read the paragraph.)"

The relevant reference in *On the origin of species* began on the last line of p. 429, but the text to which Darwin referred was on p. 430. Much of the earlier portion of the passage dealt

with Waterhouse's idea that the South American bizcacha (vizcacha or viscacha, *Octomys mimax*) was somehow related to both rodents and marsupials. We now know with great certainty that *Octomys mimax* is a rodent closely related to the chinchilla (*Chinchilla* spp), and both are placental mammals. Darwin (1859: 430) had written:

As the points of affinity of the bizcacha to Marsupials are believed to be real and not merely adaptive, they are due on my theory to inheritance in common. Therefore we must suppose either that all Rodents, including the bizcacha, branched off from some very ancient Marsupial, which will have had a character in some degree intermediate with respect to all existing Marsupials; or that both Rodents and Marsupials branched off from a common progenitor, and that both groups have since undergone much modification in divergent directions.

The pertinent phrases for Darwin were "... branched off from some very ancient Marsupial ... or ... branched off from a common progenitor". The erroneous placement of the bizcacha aside, these hypotheses are the same as those proposed in the diagrams (see Figures 4 and 5; pp 224 and 225) that accompanied his letter to Lyell. This was also why in the other two mammal trees (Figures 2 and 3; pp 221 and 222) that Darwin especially singled out rodents as nearer to marsupials.

By 1860, Waterhouse and Darwin had been corresponding cordially for at least 20 years, mostly about insects and mammals. Darwin invited Waterhouse to write the volume on living mammals for *The zoology of the voyage of H. M. S. Beagle* (Waterhouse 1839). Waterhouse had two volumes on mammals: the first included living and extinct marsupials, as well as monotremes (Waterhouse 1846), while the second was mostly about South American caviamorph rodents and various lagomorphs (rabbits and relatives) (Waterhouse 1848). Darwin provided a favourable but unsigned review of the first volume (Darwin 1847; see Barrett 1977).

Nothing in Darwin's and Waterhouse's correspondence explains Waterhouse's views on the relationship of the bizcacha and marsupials, but three of Darwin's manuscript notes, as well as the quoted passage from *On the origin of species*, provide some insight into Darwin's thinking. One manuscript note dates from 25 June 1843⁶ and the other two are passages from Darwin's 1844 essay published in *Foundations* in 1909 (Darwin 1909: 203–294, 212–213. In the 1843 manuscript note Darwin wrote:

After having read some notes Waterhouse on Mammals – I see that there are very few / intermediate / links between families ... By my theory families far apart, have descended from some remote stock & there never will be any forms intermediate between the two ... Hence we sh^d never find an exact half way between Rodents & Marsupials – but between the latter & some unknown form & Rodent & same unknown forms ... I suspect alliance of the links to other families is by saltus of a certain organ, thus Owen has discovered that vagina of Bizcacha is divided in Rodents, one of the groups taken as a whole near the Marsupiata, & – thus of this group the Bizcacha has one character much nearer. – How is this? Is each part altered separately by selection? Or old character retained? Waterhouse thinks most of the affinities between the gret [*sic*] families are "adaptive" ... Thus wombat [an Australian marsupial] is supposed to lead off by its teeth to Rodents, but teeth of Wombat really an Marsupial structure, but form of teeth merely adaptive.

Darwin was here struggling with whether similarities of organs were by virtue of their performing similar ecologic tasks or because of descent from a common ancestor. Although, as noted earlier, biologists today are more keenly aware of the problems of recognizing whether structures are a result of common descent (homology) or similar ecologic constraints (convergence), it can still be a difficult issue to resolve.

By 1844 Darwin (see Darwin 1909: 203–204) was beginning more clearly to distinguish similarities caused by common descent (Darwin's special or real affinities) versus those caused by ecological convergence (Darwin's generic, analogical, or adaptive affinities):

I have only one other remark on the affinities of organic beings; that is, when two quite distinct groups approach each other, the approach is generally generic and not special; I can explain this most easily by an

example: of all Rodents the Bizcacha, by certain peculiarities in its reproductive system, approaches nearest to the Marsupials; of all Marsupials the Phascolomys [the wombat], on the other hand, appears to approach in the form of its teeth and intestines nearest to the Rodents; but there is no special relation between these two genera; the Bizcacha is no nearer related to the Phascolomys than to any other Marsupial in the points in which it approaches this division; nor again is the Phascolomys, in the points of structure in which it approaches the Rodents, any nearer related to the Bizcacha than to any other Rodent. Other examples might have been chosen, but I have given (from Waterhouse) this example as it illustrates another point, namely, the difficulty of determining what are analogical or adaptive and what real affinities; it seems that the teeth of the Phascolomys though appearing closely to resemble those of a Rodent are found to be built on the Marsupial type; and it is animal and therefore may not show any real relation ... We shall immediately see on the theory of descent how it comes that there should be "real" and "analogical" affinities; and why the former alone should be of value in classification –

Darwin (see Darwin 1909: 213–214) generalized these ideas further:

It follows, from our theory, that two orders must have descended from one common stock at an immensely remote epoch; and we can perceive when a species in either order, or in both, shows some affinity to the other order, why the affinity is usually generic and not particular – that is why the Bizcacha amongst Rodents, in the points in which it is related to the Marsupial, is related to the whole group, and not particularly to the Phascolomys, which of all Marsupialia is related most to the Rodents. For the Bizcacha is related to the present Marsupialia, only from being related to their common parent-stock; and not to any one species in particular. ... Finally, then, we see that all the leading facts in the affinities and classification of organic beings can be explained on the theory of the natural system being simply a genealogical one.

Following the discussion of Waterhouse's ideas on the relationship of the bizcacha and marsupials, on the fourth page of his letter to Lyell written in 1860, Darwin continued:

I have not knowledge enough to choose between these two diagrams; if the Brain of Marsupials in embryo closely resembles that of placentals, I sh^d strongly prefer no^r 2, & this agree with antiquity of microlestes. As a general rule I sh^d prefer no^r I. diagram. whether or not Marsupials have gone on being developed or rising in rank from a very early period would depend on circumstances too complex for even a conjecture: Lingula has not risen since Silurian epoch, whereas other Molluscs may have risen. – Owen if he chose to attend to such view could work this out.

In contrasting *Lingula*, which has not changed since the Silurian, with "other Molluscs" that have evolved, Darwin was suggesting that marsupials similarly have not evolved as much as have placentals. It should be noted that *Lingula* is not a mollusc, but rather an inarticulate brachiopod, which is not closely related to molluscs. Nevertheless, Darwin's comparison is clear. He was saying that whereas some lineages do evolve others appear not to do so, a point that he discussed at length when describing the sole diagram in *On the origin of species* – a hypothetical phylogeny (Archibald 1997). Both in his comments on the stasis of *Lingula* and his discussion of his hypothetical phylogeny, Darwin was foreshadowing the equilibrium portion of Eldredge and Gould's (1972) idea of punctuated equilibrium.

The mention of the antiquity of *Microlestes* referred to a small Triassic mammal that Owen thought was a fossil marsupial, although we now know it is not related to marsupials or placentals. Beyond a general perception in the nineteenth century (and to some extent today) that marsupials are more primitive than placentals⁷, there is another rather convolute reason that can be pieced together as to why *Microlestes* was considered a marsupial. The molars of *Microlestes* were known only from isolated teeth presumed to be molars. The molars were formed of a series of small bumps or cusps aligned in two rows. Somewhat similar teeth are known from extinct mammals now named multituberculates. From slightly younger beds in England of Jurassic age, jaws of the multituberculate *Plagiaulax* are known. The jaws not only preserve molars with multiple cusps but also blade-like teeth

with multiple striations, which are superficially similar to teeth found in the kangaroo *Hypsiprymnodon*, hence the link between *Microlestes*, multituberculates and this small living kangaroo.⁸ Darwin's reasoning was that because *Microlestes*, as a marsupial, was older than any fossil placental, it could have been ancestral to both marsupials and placentals.

The last sentence stating that Owen could "work this out" was written in the left margin, not in the main body of the letter so I take this to be a somewhat sarcastic remark about Owen's (1857) attempts to use the degree of brain complexity to classify and rank mammals. Darwin noted that he "strongly" preferred marsupials giving rise to placentals ("Diagram II": see Figure 5, p. 000) if the "brain of marsupials in embryo closely resembles that of placentals", a reference to Owen's (1857) scheme for classifying mammals. Owen (1857) had used his perception of the organization of the brain to group mammals into four subclasses.⁹

Owen's classification was not widely accepted, notably because of his elevation of humans to their own sub-class of mammals. Huxley was especially savage in his attacks on Owen's ideas especially as they pertained to Owen's attempt to separate humans from their relatives, the apes. The "hippocampus minor" debate was won by Huxley when he showed that apes and not just humans had this structure, contrary to Owen's assertion that only humans possessed it (Rupke 1994; Owen *et al.* 2009).¹⁰

COMPARING DARWIN'S TWO MAMMAL TREES

Darwin drew the two mammal-tree diagrams on opposite sides of the single leaf which accompanied his letter to Lyell. "Diagram I" (Figure 4, p. 224) was annotated:

A. Unknown form probably intermediate between reptiles mammals, Reptiles & Birds as intermediate as Lepidosiren now is between Fish and Beatractians [Batrachians], - probably more This unknown form probably more closely related to Ornithorhynchus than to any other known form. -

On the verso ("Diagram II": Figure 5, p. 225), to the left, Darwin wrote "A (as on other side)". On both diagrams an "A" was positioned at the origin of each tree; thus, the above description was intended to be the ancestor in both trees.

The two main branches of "Diagram I" are more symmetrical than in "Diagram II" (Figures 4 and 5), and the relative lengths of the branches vary slightly. The topology or relative positions of the branchings in the two diagrams are almost identical except that the first node in the marsupial side is flipped. In total, these differences appear to be inconsequential to Darwin's intentions. I also cannot attribute any significance to the fact that both diagrams open downwards. He may simply have begun each tree at the top the page and opening them downwards because the parts of the tree he wished to emphasize were their bases.

The higher taxa listed as terminal branches are identical in the two diagrams except for minor differences such as capitalizations. As Darwin's intent, made clear by his description, was the question of the ancestry of placental and marsupials, I do not think one can give any particular credence to any details of the terminal branches.

In "Diagram I", on the "True Marsupial" branch "Kangaroo fam." and "Didelphys fam." refer to what we today essentially recognize as the families Macropodidae and Didelphidae, respectively, although the content of each group in Darwin's time was somewhat broader. On the placental side, the first branch was "Rodents" with "Insectivores" as the second

branch. There is then a three-way split between one branch with "Ruminants" and "Pachyderms" (thick-skinned mammals), the second for "Carnivores", and the third for "Quadrumana". The orders Rodentia and Carnivora are recognizable. Insectivora tended to include any small placental mammals with sharp teeth that could not be aligned with any other placentals. It was what has been termed a "wastebasket taxon" for obvious reasons. In modern classification, Insectivora is often not used, but its historical descendant is Lipotyphla or Eulipotyphla including shrews, moles, hedgehogs, and few lesser known groups.

Finally, "Quadrumana" (referring to four hands) was proposed by Blumenbach (1779) for all primates except humans in contradistinction to his "Bimana" (two hands) for humans. The names were out of favour by the end of the nineteenth century. Huxley (1863) argued convincingly that the so-called higher apes were reasonably put in Linnaeus's Primates along with humans. Huxley, as well as others, realized that humans belonged to the same order as all other primates and that apes in particular had a special relationship to humans. It is not certain what Darwin meant by "Quadrumana" in his 1860 sketch. In *Descent of man*, Darwin (1871: **1**: 190) continued to use Quadrumana for non-human primates but cited the argument that these should be united with humans in a single order called Primates.

The most interesting aspects of the two trees are not Darwin's views of the relationships within marsupials and within placentals, but rather the alternative hypotheses he presented regarding the origin of marsupials and placentals. On "Diagram I" (Figure 4, p. 224) above the split between "True Placental" and "True Marsupial" he wrote "Mammals not true marsupials not true placentals." In "Diagram II" (Figure 5, p. 225) the earliest ancestor is labelled "true Marsupials lowly developed" followed by "True Marsupials higher developed?" with the split leading to "Placentals" and "Present Marsupials".

As described earlier, in his letter Darwin indicated to Lyell that as a general rule he should prefer the tree in "Diagram I", but if the embryological brain of marsupials closely resembled that of placentals he should strongly prefer the tree in "Diagram II" as this agreed with the antiquity of *Microlestes*. We now know that marsupials did not give rise to placentals, but rather they share a common ancestor as Darwin indicated in "Diagram I". Although it would be tempting to suggest that Darwin favoured one of the trees over the other, especially if it were the correct version shown in "Diagram I", the evidence in his letter and elsewhere is not definitive on this matter. The best we can argue, based on current evidence, is that Darwin did weigh alternative views for the monophyletic versus the successive origin of living mammals, which no one else was doing with the same acumen 150 years ago.

CONCLUSIONS

The only known competing phylogenetic trees that Darwin produced occur at the end of his 23 September 1860 letter to Charles Lyell. In this letter (and based on earlier writings) he clearly argued that living marsupials and placental mammals are monophyletic or share a single ancestor rather than that various placental groups having arisen successively from various marsupial-like mammals. The two alternative phylogenetic hypotheses argued a true but "lowly developed" marsupial gave rise to both "present marsupials" as well as placentals, or the common ancestor of marsupials and placentals was neither a marsupial nor a placental mammal. The former of the two hypotheses appears to have been influenced by Richard Owen's views on mammalian brain evolution and the ancient fossil remains of the supposed marsupial *Microlestes*. Neither of these ideas is now accepted. The latter of Darwin's two hypotheses appears to have been influenced by what Darwin perceived as evolutionarily derived similarities that separately unite marsupials and that unite placentals. Although these perceptions have proven to be true, Darwin did not decide between the two hypotheses. The more general theme is that Darwin's ruminations on this topic made him a strong advocate for monophyly or single origin, rather than the successive or continuous creation or origin of major animal groups, including mammals.

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NOTES

¹ Charles Darwin to Charles Lyell, "Sun. 23" [September 1860]; original ms. in American Philosophical Society (APS B D25.L). Transcriptions given in this paper are by the present author using a copy of the original manuscript, with consultation of the transcription of the same letter in Burkhardt *et al.* (1993: 337) and Darwin (1877: 343). References to pagination are from the original manuscript.

A full transcript can be found in Burkhardt *et al.* (1993: 377–381), and online at the Darwin Correspondence Project (URL http://www.darwinproject.ac.uk/entry-2925 accessed 12 December 2011).

² DAR80:B91r: original ms, Cambridge University Library (hereafter CUL).

³ DAR205.5:183r: CUL.

⁴ DAR205.5:184v: CUL.

⁵ Hans-Dieter Sues to JDA, pers. comm., 26 September 2011. Sues indicated that in his reading of Owen's work he has found no evidence that Owen opposed the idea of mammalian monophyly. Rather, Owen talked about change in terms of what we now call grades, which were based heavily on his flawed classification based on gross brain structure. Further, Sues notes that Owen was close to understanding mammalian origins, as he increasingly realized the connection between the South African therapsids and mammals, whereas T. H. Huxley tried to derive mammals from amphibians, based especially on shared possession of double occipital condyles while he steadfastly ignoring Owen's therapsids. See also Desmond (1982), on why Huxley's rejected Owen's so-called mammal-like reptiles as intermediates between amphibians and mammals.

⁶ DAR205.5:88r, 88v, 89: CUL.

⁷ The idea that marsupials are primitive or inferior to placentals remains in popular culture. A sign (as of 1 October 2011) in front of one of the enclosures at the world-renowned San Diego Zoo reads, "Australia's best known animals are pouched (marsupials). At the time Australia broke away from the other continents, the higher mammals (placentals), had not yet evolved, and marsupials were able to develop free of competition."

Marsupials reached Australia by at least 55 million years ago, and probably earlier, but the place they came from, South America (via Antarctica) harboured a wealth of small to large omnivorous and carnivorous marsupials, while the placentals were their prey. Old ideas do die hard.

⁸ The name *Microlestes* was proposed for these Triassic teeth in 1847, but the name was preoccupied by a beetle so the name *Thomasia* proposed in 1908 took its place. *Thomasia* is now known to be only distantly related to living mammals, including both marsupials and placentals (Kielan-Jaworowska *et al.* 2004).

⁹ Owen (1857) had used his perception of the organization of the brain to group mammals into four subclasses. *Lyencephala* (meaning loose brains) – monotremes and marsupials – were relatively small, had a smooth cerebrum, and the two hemispheres had little connection. *Lissencephala* (smooth brains) had a corpus callosum joining the two cerebral hemispheres (common to all placentals) but the cerebrum had few convolutions; examples included rodents, bats, xenarthrans and lipotyphlans. *Gyrencephala*, referring to the gyri or convolutions of the cerebrum that were relatively larger and covered the cerebellum, included all remaining placental mammals, except humans. Finally, the large-brained humans were the only species assigned to the sub-class *Archencephala* (ruling brain).

 10 The hippocampus minor of Owen and Huxley is now called the calcar avis. It is an involution of the ventricular wall produced by the calcarine fissure (Owen *et al.* 2009).

¹¹ URL http://darwin-online.org.uk/ accessed 12 December 2011.

¹² URL http://janus.lib.cam.ac.uk/db/node.xsp?id=EAD%2FGBR%2F0012%2FMS%20DAR accessed 12 December 2011.

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NOTE ADDED IN PROOF

After completion of this paper, another Darwin sketch emerged including mammals (DAR205.6.51r: Cambridge University Library). Drawn on the back of a stationer's advertisement, it includes five tree sketches, one about pigeons and the other four about mammals. One mostly crossed out sketch may have been about mammal origins, another two closely set trees deal with mammalian ruminants and carnivores, and the last of the four mammal trees is a single tree dealing with these two groups of mammals. Other comments and labels on the sketch show Darwin's thinking about how embryological development related to his ideas of evolution. This sketch is included in a chapter on Darwin's trees in a book in preparation by the author dealing with ladders, trees, and other imagery of nature's order.