A reappraisal of Charles Darwin's engagement with the work of William Sharp Macleay

Aaron Novick

Forthcoming in *Journal of the History of Biology*

Abstract

Charles Darwin, in his species notebooks, engaged seriously with the quinarian system of William Sharp Macleay. Much of the attention given to this engagement has focused on Darwin's attempt to explain, in a transmutationist framework, the intricate patterns that characterized the quinarian system. Here, I show that Darwin's attempt to explain these quinarian patterns primarily occurred before he had read any work by Macleay. By the time Darwin began reading Macleay's writings, he had already arrived at a skeptical view of the reality of these patterns. What most interested Darwin, as he read Macleay, was not the quinarian system itself. Rather, Darwin's notes on his reading primarily concerned certain background principles animating Macleay's work, in particular: (a) the non-existence of a *saltus* between human and animal minds, (b) the difficulty of establishing boundaries between species and varieties, and (c) Macleay's method of variation. Darwin's interest in the last of these left a mark on his discussion of taxonomic methodology in the *Origin*.

1. Introduction

The old view that Darwin could not possibly have been interested in William Sharp Macleay's "mystical" or "numerological" quinarian system of classification (De Beer 1963; Ghiselin 1969) is no longer tenable, thanks to two fine studies that reveal the interest with which Darwin engaged

with Macleay's ideas (Ospovat 1981, 101–13; Di Gregorio 1996).[1] These studies appear to have convinced even some of the skeptics. Ghiselin for instance, now grants that Darwin "gained much from Macleay" (2004, 165). But what, exactly, did Darwin gain? While both Ospovat and Di Gregorio have illuminated Darwin's engagement with Macleay's ideas, an important aspect of this engagement remains unnoticed. This paper aims to bring this aspect to light.

The most striking feature of Macleay's quinarian system is the intricacy of its patterns. Macleay grouped all organisms into nested, circular groups, each of which contained five subgroups. Moreover, the subgroups of contiguous circles, when laid out in parallel, showed analogical resemblance relations (explained in more detail below). Popular but controversial in the 1820s and 1830s, this elaborate system occupied Darwin's attention throughout much of the period during which he maintained his species notebooks.[2]

Both Ospovat and Di Gregorio primarily consider Darwin's relationship to these quinarian patterns. Ospovat argues that Darwin, early in his species notebooks, took for granted that much of Macleay's work was basically accurate, seeking not to refute it but to explain it using transmu-

[1] All future references to Ospovat (1981) are to this page range, unless otherwise indicated.

[2] These notebooks can be found in Barret et al. (2008). In-text page citations will be to the journals themselves and not to the volume that contains them; e.g., C notebook page 73 will be cited as C73. A guide to interpreting quotes from this volume: ‹text crossed out›; «text added in at the initial time of writing»; **text added at a later date**. I use a double slash (//) to indicate a page break in Darwin's notebooks. Given the frequency with which spelling and grammatical errors appear in Darwin's notebooks, I will not bother highlighting them.

tationist principles. Di Gregorio, looking more narrowly at Darwin's "abstract" of *Horæ Entomologicæ* (Macleay 1821), argues that Darwin picked bits and pieces of Macleay's work to reinterpret in a transmutationist vein, discarding the rest. Di Gregorio (1996, 105) focuses especially on how Darwin added a temporal dimension to Macleay's "one-dimensional" (i.e., atemporal) representation of nature.

Both accounts are basically accurate, but neither tell the whole story. Ospovat's account participates in a bias common in the literature surrounding Macleay: it focuses on the quinarian system's intricate patterns while neglecting Macleay's underlying philosophical and methodological commitments. Di Gregorio pays more attention to Darwin's interest in these commitments, but because he focuses on Darwin's reading of a single text, his study does not capture the way that Darwin's engagement with Macleay changed over time.

My goal in this paper is to provide an account of Darwin's engagement with Macleay that (a) emphasizes Darwin's interest in Macleay's philosophical commitments and (b) captures the dynamics of Darwin's attempt to think through Macleay's ideas. In particular, I argue that Darwin showed as much interest in Macleay's philosophical commitments (what I call "quinarian principles") as he did in Macleay's beliefs about patterns in the natural system ("quinarian patterns"). As I will show, there is an important trend in Darwin's engagement with the quinarian system. In the B notebook, at which point Darwin had not yet read Macleay's work, Darwin focused on trying to explain away quinarian patterns. In the C and later notebooks, Darwin began reading Macleay's work. Interestingly, most of his notes on his reading did not concern quinarian patterns, about which he was becoming increasingly skeptical. Rather, they focused on Macleay's underlying commitments, often treating them quite sympathetically. There was thus a shift in emphasis in Darwin's engagement with Macleay's ideas, from an interest in quinarian patterns to an interest in

quinarian principles, and this shift coincided with Darwin beginning to read Macleay's work. Moreover, I will argue, Darwin's interest in quinarian principles had a small but enduring influence on his discussion of classification in the *Origin*.

2. Macleay's quinarian system summarized

William Sharp Macleay, a British entomologist, developed the quinarian system in the late 1810s and published it in *Horæ Entomologicæ* (Macleay 1821). The first part of that work (published 1819), a monograph on scarab beetles, showed how the Linnaean genus *Scarabaeus* could be organized into circles of five subgroups each. The second part (published 1821) programmatically extended the patterns Macleay believed he had discovered in scarabs to the rest of the animal kingdom. In the 1820s and 1830s, the quinarian system was the subject of much discussion and much acrimony, as naturalists sorted through its merits and demerits. Given its prominence in discussions among natural historians of the time, it is no surprise that Darwin felt the need to work through it for himself, as Ospovat (1981) has shown.

Macleay's system was built around six central claims (for a full account, see Novick 2016). First, Macleay (1821, 362–64) argued that resemblances among groups (both species and groups of higher rank) can be separated into two kinds, affinity and analogy. Two groups are related by affinity if they are primarily similar, but differ in certain particulars, as in the case of two beetle groups with similar overall morphologies, but slight differences in the structure of the mandibles (e.g., *Geotrupidæ* and *Scarabæidæ*; Figure 1). Two groups are related by analogy if they are primarily different, but are similar in one or a few striking particulars, as in the case of two beetle groups that are quite dissimilar, but have similarly structured mandibles (e.g., *Geotrupidæ* and *Rutelidæ*; Figure 1).

Second, all natural groups form circular chains of affinity (Macleay 1821, 164–65). In the circle of Vertebrata, for instance, there is a linear chain of affinity connecting Pisces to Mammalia through Amphibia, Reptilia, and Aves. This chain is made circular by the existence of a further affinity between Mammalia and Pisces, causing the chain to "return into itself," to use Macleay's (1821, 335) characteristic language (Figure 2). Third, each group is characterized by a type. In each group, two normal subgroups most resemble the type, while three aberrant subgroups deviate from the type. Fourth, adjacent circles inosculate; i.e., chains of affinity are not restricted within circles, but also cross into adjacent circles (Macleay 1821, 318). They do so by passing through osculant groups (e.g., Cephalopoda, Figure 2), which do not fall into either of two adjacent circles. Macleay argued that osculant groups tend to have few species. Fifth, each group has five subgroups, as well as five osculant subgroups connecting them (Figure 1; Figure 2).[3] Sixth, contiguous circles show parallel relations of analogy (Macleay 1821, 362–64). That is, each subgroup in one circle has a relation of analogy to the subgroup in the corresponding position of an adjacent circle.

For Macleay, the natural system of classification should place groups next to those to which they share the closest affinity, and Macleay (1821, 363) traced the errors of many prior naturalists to their mistaking analogies for affinities. The first of the six features above is thus the most central element of Macleay's system. The other five features describe the patterns that Macleay believed would characterize any arrangement that respected the affinity/analogy distinction. They were regularities he discovered as a result of distinguishing affinities from analogies.

From this point on, I will refer to these six features as "quinarian patterns." One might argue

[3] Note that Figure 1, from the first part of *Horæ Entomologicæ*, lacks any osculant groups. These were not added until 1821, in the second part of that work.

that the affinity/analogy distinction is more properly a principle than a true pattern, but there is good reason to group it with the other five claims. Before Darwin actually read Macleay's work, his engagement with Macleay's ideas stemmed from other naturalists' summaries of the quinarian system. The papers of the time that discussed Macleay's work—whether written by supporters (e.g., Swainson 1835), neutral commentators (e.g., Jenyns 1835), or opponents (e.g., Montagu 1831, xxxiii–lv)—focused predominantly on his affinity/analogy distinction, in conjunction with (usually a subset of) the other five features. By contrast, the features of Macleay's thought that I describe under the heading "quinarian principles" were not so widely discussed, and Darwin would have had to read Macleay's work (or talk to Macleay directly) to learn about them.

3. Chronology of Darwin's engagement with Macleay

Darwin appears to have first encountered Macleay's work during his time as a student. At the very least, he knew of it by 1832, as he used the quinarian term of art "inosculating" in a letter to Henslow (Darwin to J. S. Henslow [*c.* 26 October –] 24 November [1832]. Letter 192).[4] In 1836, both Darwin and Macleay returned to Britain: Darwin from the Beagle voyage, Macleay from a ten-year stint in Cuba. Macleay apparently urged Darwin to publish an account of his voyage (Ospovat 1981, 108). Their overlap in Britain lasted roughly two years, as toward the end of 1838 Macleay moved to Australia (Holland 1996).

When, in 1837, in the B notebook, Darwin began discussing quinarian ideas, he did not reference particular texts by Macleay, and there is no known evidence that Darwin had, at this point,

[4] This and all subsequent letters are cited by the author, recipient, date, and letter number as provided by the Darwin Correspondence Project: https://www.darwinproject.ac.uk.

ever read Macleay's work. Importantly, while Macleay was in Cuba, the quinarian system was primarily promoted by Nicholas Vigors (especially from the mid-1820s to the early 1830s) and William Swainson (especially in the latter half of the 1830s), the latter of whom defended a version of the system quite different from Macleay's (Swainson 1835; see Lowther 2016). Moreover, given the rarity of *Horæ Entomologicæ*, most copies of which were destroyed in a bookseller's fire on March 02, 1822 (Macleay 1830a, 3; Reider 1841, 302), it is almost certain that Darwin had not read Macleay's most important text at the time he was maintaining the B notebook. During this time, Darwin did read a work by William Swainson (B92). Inside the back cover of the B notebook, Darwin made a note that he should read *Horæ Entomologicæ*, and in May 1838 he made a special trip to read one of the surviving copies (Di Gregorio 1996). The first explicit reference to a text by Macleay occurs on C42 (c. February or March 1838). Darwin there cited Macleay's letter to Bicheno, as well as a short paper on the genus *Capromys* (Macleay 1829a, 1829b). Darwin's final reference to Macleay in the species notebooks appears on E22-23 (written October 14, 1838); there is also a trivial reference to *Horæ Entomologicæ* on ZEd18 (also from 1838). All of Darwin's reading of Macleay thus appears to have occurred in 1838.

As Ospovat (1981) has shown, the seriousness with which Darwin treated the quinarian system tracks the general regard for that system in Britain. During the late 1830s, numerous publications debated the system's merits and demerits, and it received serious attention in Leonard Jenyn's (1835) relatively neutral paper on the "Recent Progress and Present State of Zoology." The popularity of the system declined rapidly after Strickland's critical presentations at the 1840 and 1843 meetings of the British Association for the Advancement of Science (Strickland 1841, 1845; see McOuat 1996; Lowther 2016, xxx). This coincided with the emigration (Macleay, Swainson) or death (Vigors) of the system's most prominent followers between 1838 and 1840 (McMillan and

Cernohorsky 1979; Novick 2016). Thus, the entirety of Darwin's engagement with Macleay's work in the species notebooks (maintained from July 1837 to July 1839) occurs during this final wave of interest in the quinarian system before its rapid collapse.

4. The B notebook: explaining away quinarian patterns

4.1. The first engagement with Macleay in the B notebook

In the B notebook (July? 1837–March? 1838[5]), Darwin's engagement with the quinarian system was primarily limited to attempts to explain certain quinarian patterns. As Ospovat (1981) has already looked at this in detail, a full tour of the B notebook here is unnecessary. I will therefore focus on a few key passages that will allow me to highlight certain important themes and to articulate one point of disagreement with Ospovat.

Darwin's first reference to Macleay's ideas appears on B23, where Darwin introduced the notion of a "triple branching in the tree of life owing to three-elements air, land & water." This is the first mention of what Darwin later came to call his three-element theory. This theory explained why there should be "points of affinity in each branch" (B24), and Darwin later invoked the theory to explain why some but not all groups have five sub-groups. The theory was a major component of Darwin's attempt to address Macleay's ideas in his work, and it deserves close scrutiny.

Just before introducing the three-element theory, Darwin considered the kind of natural process that could maintain relative constancy in the number of existing species over time (B20-22). He

[5] For B notebook chronology, see Barrett et al. (2008, 167). The July 1837 start date is especially uncertain.

suggested that "branches dying out" (i.e., extinction) could match the rate of the production of new species. A few pages later, Darwin tied extinction into his three-element theory. On B25, Darwin considered whether "fish & penguins really pass into each other." Though Aves and Pisces were not contiguous groups for Macleay (figure 2), this was the sort of transition that the quinarians had highlighted.[6] More broadly, the idea that groups "pass into each other" is an essential element of any continuous system, whether linear or quinarian.[7] Darwin, who was in the process of temporalizing the notion of continuity (Di Gregorio 1996), needed to think about how this would impact the notion of gradual transitions between groups. In response to this question, Darwin drew a diagram representing how "fish can be traced right down to simple organization. — birds— not" (B26). The diagram shows two unlabeled branches, one (fish) solid all the way back to the origin, the other (birds) disconnected from the ancestor by a dotted line indicating extinction.

At this point, the three-element theory comes in. In thinking about how extinction would shape the tree of life, Darwin made his famous reference to the "coral of life." The history of life is best represented by a coral because "bases of branches dead; so that passages cannot be seen" (B25). Darwin illustrated this with a triply branching diagram, thereby simultaneously illustrating his three-element theory (B26). On the subsequent page, Darwin argued that extinction could explain why some groups appeared circular:

> We may fancy, according to shortness of life in species that in perfection, the bottom of branches dead.—*so that* in Mammalia «birds» it would only appear like

[6] Swainson (1835, 320–21), for instance, argued that penguins and tortoises are contiguous groups.

[7] For Macleay's views on continuity, see Novick 2016, 110-17.

circles;— & insects amongst articulata.—but in lower classes, perhaps a more linear arrangement.— (B27)

These eight pages in the B notebook show Darwin grappling with a number of issues that his evolutionary theory would have to explain or otherwise accommodate. What is the role of extinction in evolution? How can the history of life be best represented? What happens when continuity is temporalized? In the midst of all this, Darwin was engaging with the quinarian system. This is true not just because of the three-element theory (which Darwin had not yet invoked to explain quinarian patterns), but also because of Darwin's attempt to explain why some groups appear circular. The particular groups Darwin chose are revealing: insects, birds, and mammals. Macleay was an entomologist, his two most prominent followers (Nicholas Vigors and William Swainson) were ornithologists,[8] and John Gray had proposed a quinarian arrangement of Mammalia (Gray 1825c).[9] Darwin, in other words, did not explain why just any group should appear circular. He explained why precisely those groups that the quinarians had most prominently arranged should appear circular. In "lower classes" such as fish, where the class "can be traced right down to simple

[8] Lowther (2016, 64) argues that, thanks to Vigors' efforts, the Quinarian system was "almost exclusively identified with ornithology in the 1820s and 1830s."

[9] While Gray does not cite Macleay in that paper, he divides the mammals into five orders, each containing five families, two of which are typical and three of which are aberrant, and he explicitly comments on certain groups being "parallel in analogy" (Gray 1825c, 343). Moreover, in his arrangement of the reptiles and amphibians (Gray 1825a, 194), he explicitly credits Macleay with having shown that "the order of this class appears to assume a circular disposition." See also his quinarian arrangements of butterflies, mollusks, and echinoderms (Gray 1824a, 1824b, 1825b).

organization," a linear arrangement would suffice.[10]

4.2 Explaining away the quinarian system

Darwin's engagement with the quinarian system was integrated into his general evolutionary thinking at the start of the species notebooks. Darwin attempted to address several distinct concerns using his early evolutionary theory. The quinarian system was merely one of these concerns. At this point, two questions arise. First, how did Darwin's explanations of quinarian patterns actually work? Second, to what extent did Darwin accept the quinarian system at this point in the notebooks? In answering the first question, we will see that Darwin accepted the quinarian system in only a very limited sense (contra Ospovat). From the start, he was not so much explaining quinarian patterns as explaining them away.

Darwin's explanation of circularity is more straightforward than his three-element theory, so let us begin there. Extinction plays the crucial explanatory role. On B26, he noted that fish can, while birds cannot, be "traced right down to simple organization"—that is why birds admit of a circular arrangement, while fish do not (B27). Darwin did not elaborate on the details of this explanation, but it may have worked as follows. Imagine a single ancestral species that gives rise to five descendant species, each of which diverges from it to some degree. The descendant species might then be arranged in a circle around the ancestor. If the ancestor then goes extinct (as occurs in some but not all groups; see B26), the remaining species would appear to form a circle. As for why it is the ancestor specifically that goes extinct, Darwin explicitly connected this to the increased perfection of the descendants: "in perfection, the bottom of branches deaden" (B27). That

[10] Macleay (1842) did eventually try his hand at the fishes.

is why the circular disposition is seen in more advanced classes (mammals, birds, and "insects amongst articulata"), but not "in lower classes" (B27).

The three-element theory poses more difficult interpretive issues. How, exactly, can a triple branching in the tree of life explain why certain subgroups should have five subgroups? Darwin never explicitly laid out his reasoning. The best indication of his view comes at B23: "the endeavor of each ‹one› typical class to extend his domain into the other domains. & subdivision ‹six› three more, double arrangement.—" This is obscure, but one way to read the passage is as suggesting that, after a group splits into three forms (aquatic, terrestrial, and aerial), one of these groups (the "typical class") will then undergo a triple branching again. Since it is already adapted to one of the three-elements, this will produce two further groups, yielding a total of five (Figure 3, left side).[11] This matches the interpretation of Jonathan Hodge (2013, 67). Unfortunately, the interpretation

[11] This view admits of two distinct interpretations. On the first interpretation, each branching involves an ancestral species that expands from its initial element (whichever that might be) into two further elements. On this view, the ancestor persists. This view fits especially well with Darwin's comment that the process is driven by the typical class "extend[ing] his domain into the other domains" (B23). On another interpretation, the first branching involves the ancestor producing three descendant species, then going extinct. One of these descendants then gives rise to the second branching, and itself goes extinct. This view fits especially well with Darwin's view that the groups that admit of a quinarian arrangement tend to have extinct rather than extant ancestors (B26-27). I do not see that any evidence is decisive. The difficulties for Darwin's three-element theory that I will discuss below apply equally to both interpretations. Thanks to an anonymous reviewer for pressing the issue.

faces an important problem.

The primary reason to support this interpretation is that it appears to be the only way to make two triple branching events yield five groups. But Darwin did not restrict the three-element theory to explaining why some groups have five subgroups. Later, in discussing the quaternarian system of the mycologist Elias Fries, he attributed Fries' emphasis on the number four as the result of the lack of aerial forms among the cryptogamous flora:

> If my idea of origin of quinarian system is true, it will not occur in plants which are in far larger proportion terrestrial,—if in any in the Crytogamic flora **but not atmospheric type. Hence probably only four, is not this Fries rule— What subject has M^r^ Newman the (7) Man studied**

If two triple branchings yield five groups, two double branchings should yield three groups (figure 3, right side). Only if both the aquatic and terrestrial forms from the first branching undergo a second branching will four total subgroups result, but in that case there are three branchings, not two. This is true regardless of whether one interprets the ancestors of each branching as persisting or going extinct (see footnote 10).

There thus appears to be no way to consistently interpret Darwin's three-element theory while simultaneously preserving its ability to do the explanatory work Darwin required of it. The basic difficulty is that Darwin needs some way of explaining how two triple branchings yield five rather than six groups. Whatever mechanism explains this, if it operates in the case of double branching, it should lead to the production of three groups, not four. In the end, we may have to accept that Darwin never worked out a fully consistent version of his three-element theory before he eventually abandoned it, sympathizing with Darwin's own eventual judgment that the whole endeavor of explaining quinarian patterns with the theory was a "hallucination" (quoted in Ospovat 1981, 113).

We are now in a position to see why Ospovat's claim that Darwin, in the B notebook, accepted Macleay's work as "more or less right" is an overstatement. Darwin did not accept the reality of the patterns Macleay believed he had found in nature—at least, he did not accept them in the same form in which Macleay proposed them. His project in the B notebook was not to explain how such patterns could arise but to explain how the appearance of such patterns could arise. I mean more by this than the claim that Darwin replaced Macleay's universal regularities with regularities of limited scope. Even in those cases where Darwin accepted Macleay's findings to some degree (mammals, birds, insects), he accepted only the appearance of those patterns, not their reality.

This is especially clear in the case of Darwin's explanation of circularity. As we saw, it was the extinction of the ancestor that played the crucial role in Darwin's explanation. Groups appeared circular precisely because the ancestral species (which would be in the center of the circle) was excluded from the circle. As Di Gregorio (1996, 105) notes, the circles are formed by "cutting Darwin's trees through (abstract) 'one-dimensional' present time rather than (real) time ('two-dimensional' past and present)." Macleay's circles, however, were two-dimensional, capturing atemporal patterns of affinity among all natural groups, regardless of when those groups existed. For example, Macleay (1840) argued that trilobites complete the quinarian circle of Crustacea. Darwin, however, sought only to explain the appearance of a circular disposition within currently existing groups. The appearance of circularity, for Darwin, was produced by incompleteness, by the exclusion of the ancestor from the classification, whereas for Macleay circular patterns would appear only when knowledge of a group was complete.

Darwin's use of his three-element theory to explain why certain groups have five subgroups is similarly removed from the pattern Macleay believed he had discovered. While it does explain why one would find five subgroups at a given rank, Macleay believed that groups at all ranks had

five subgroups. It would certainly be possible to explain this with the three-element theory. Simply assume that, within each group, whatever the rank, that one typical form that lives in one element expands, twice over, into the other two elements. Note, however, that applying the theory in this way makes a strong prediction: each group of five, at every rank should contain terrestrial, aquatic, and aerial forms, with, for example, one terrestrial subgroup and two each of aquatic and aerial subgroups.[12] This is manifestly untrue of Macleay's actual groupings, starting with his original quinarian classification of terrestrial scarabs (figure 1), and there is no reason to attribute such an implausible belief to Darwin.

Importantly, Darwin never applied his three-element theory at so fine a grain. When Darwin introduced the theory at B23-24, he only applied it to "each main stem" of the tree, and used it to explain why there are "points of affinity in each branch" (B24). He made no suggestion of a series of triple-branchings at every rank. The famous "I think" diagram on B36 shows a variety of branchings, many of them triple, but others double, quadruple, or quintuple. On B43, the three-element theory returns, again simply to explain "affinities from three elements." The discussion of Fries at B45-46, cited above, discusses the non-application of the quinarian system to plants at a similarly general level. The brief mention of the three-element theory at B112 is likewise general.

In sum, then, Darwin's three-element theory is suited only to explaining why groups that have expanded into all three elements may have a tendency to have five subgroups, but it is ill-suited to explain the genuine quinarian pattern of all groups at all ranks having five subgroups. Moreover,

[12] It does not matter which particular type was represented by only one subgroup: the "dominant" subgroup that undergoes the second branching might vary by group. The key point is that the 1-2-2 pattern should be seen in every group.

Darwin never attempted to apply his theory at such a fine grain. Darwin did not appear to have treated triple branching as a universal pattern even in those groups that had extended into all three elements. Rather, what his three-element theory explains is why there should be an imperfect tendency to see five subgroups per group in certain regions of the tree of life. It is rather unsuited for the sort of fine grained application that a commitment to Macleay's having been more or less right would have required.

4.3. The remainder of the B notebook

Two further aspects of the B notebook deserve discussion. The first concerns Darwin's understanding of affinity and analogy. The second concerns Darwin's understanding of osculant and aberrant groups.

On B112, Darwin integrated his three-element theory with his reflections on Cuvier: "Cuvier's theory of *Conditions* of existence is thought to account resemblances & ∴ quinary system, or three elements." Because similar conditions of existence require similar functional modifications, there will be certain resemblances among terrestrial species, among aquatic species, etc. Darwin continued:

> With unknown limits, every tribe appears fitted for as many situations as possible.
> for instance take birds animals,[13] reptiles fish— **Conditions will not explain status**
> (perhaps consideration of range of capabilities past & present might tell something)
> (B113)

[13] Darwin seems to have written "animals" where he meant "mammals," a mistake he also made at B43.

Without using the term 'analogy,' Darwin here explained why analogies could not "explain status," i.e., determine in which group a species should be classified. Sixteen pages later, Darwin made the connection to analogy explicit:

> The relation of Analogy of Maclay &c. appears to me the same as the irregularities in the degradation of structure of Lamarck, which he says depends on external influences.— For instance he says wings of bat, are from external influence.— // Hence name of analogy, the structures in the two animals bearing relations to a third body, or common end of structure (B129-130)

Analogous structures, for Darwin, are not related simply to each other, but also to a "third body." The wings of birds and of bats, for instance, are both related to the air, namely to the "common end" of flight.[14] Because analogies are related to a common end, they cannot indicate affinities (i.e., shared descent). As Darwin put it: "Mere length of bill does not ‹indicate affinity with snipes› indicate affinity, because similar habits produce similar structure" (B162).

Regarding osculant and aberrant groups, Darwin quoted George Johnston on "that axiom in Natural History that all aberrant & osculant groups are not only few in species, but every two or three these form genera" (B126). This passage shows Darwin encountering, via the writings of a non-quinarian, one of the patterns that Macleay had found in nature: that osculant groups have few species. At this point, Darwin presumably did not know that Macleay had made this argument, as he had not yet read *Horæ Entomologicæ*. Darwin attempted to explain why this should be so: "**this**

[14] See the editor's note to B130, available online at: http://darwin-online.org.uk/content/frameset?pageseq=132&itemID=CUL-DAR121.-&viewtype=side (Accessed May 4, 2018). This footnote does not appear in the printed edition.

is «from unfavourable conditions» there are many gaps. &c those forms which «nevertheless» have produced species, have produced fe[w]" (B126). The brevity of this explanation makes it opaque, but Darwin appears to have thought that osculant groups tend to face unfavorable conditions, such that, when they do manage to survive and produce new species, they produce few.

With that, we may leave the B notebook. We have seen how Darwin integrated his reflections on the quinarian system of classification into his burgeoning evolutionary theory. These reflections primarily took the form of trying to explain why quinarian arrangements could appear plausible without accepting their reality. These explanations were integrated with Darwin's attempt to think through other issues as well: constancy in the number of species, progressive development, and Cuvier's conditions of existence.

5. The C, D, and E notebooks: patterns waning

Moving to the later species notebooks, we can track several important changes.[15] Most notably, Darwin began reading Macleay's texts. Second, Darwin's skepticism of the quinarian system increased: he began to seriously doubt that quinarian patterns were even apparent, let alone real. Accordingly, he de-emphasized attempts to explain away those patterns. At the same time, third,

[15] The C notebook was maintained between March and July 1838, with much of the notebook (C100-256) written in a five-week period between mid-May and mid-June (Barrett et al. 2008, 237–38)—note that Darwin read *Horæ Entomologicæ* in the first half of May 1838 (Darwin to Susan Darwin 15 May [1838]. Letter 413; Di Gregorio 1996). The D notebook was maintained from mid-July to early October 1838 (Barrett et al. 2008, 329–30), and the E notebook was maintained from October 1838 to July 1839 (Barrett et al. 2008, 395–96).

Darwin picked out passages from Macleay's texts in which Macleay expressed certain principles (e.g., about the nature of species and the methodology of classification) to which Darwin was sympathetic. The aim of this section and the next is to document Darwin's shift in focus from quinarian patterns to quinarian principles and to show how this pattern related to Darwin's reading of Macleay. This section focuses on Darwin's waning interest in quinarian patterns; the next details his emerging interest in quinarian principles.

In the previous section, we saw that the Darwin of the B notebook attempted to explain: (a) why, in at least some groups, there tended to be a regular number of subgroups; (b) why certain groups appeared to admit of a circular arrangement; and (c) why osculant groups tended to have few species. In the later notebooks, Darwin's already meager belief in the reality of (a) and (b) faltered further, while he expanded further on his explanation of (c). The next three subsections take up these three topics in turn.

5.1. Moving away from the three-element theory

In the B notebook, Darwin was somewhat sympathetic to Macleay's claim that all groups have an equal number of subgroups, granting it partial legitimacy within the groups quinarians had studied. In the C notebook, Darwin's sympathy almost wholly vanished. Take, for instance, this passage from C73-74:

> These «aberrant» varieties will be formed in any kingdom of nature, where scheme not filled up, (most false to say no passages; nature is full of them.— wading birds partially webbed &c. &c.—)— & in round of chances every family will have some aberrant groups.— but as for number five in each group absurd.— the mere fact of division of lesser & more power (2.typical 3.subtypical) // where power arbitrary.

leaves door open for Quinarians to deceive himself.

Darwin here treated aberrant groups as those that deviate from the "type" of their group because they have become adapted to circumstances other than those their ancestors faced, often to fill an empty place in nature's "scheme."[16] Darwin explained why every family should have some aberrant subgroups ("the round of chances"), but denied that there should be any regularity in the number of such groups in each family.[17] At the end of this passage, for the first time, Darwin suggested that much quinarian work, so far from being even superficially right, rested instead on self-deception. On C170, Darwin expressed similarly negative sentiments, referring to Swainson's exposition of the quinarian system: "observe the character of the *demonstrations* offered of the singular views there offered, & he must be a zealous man in the cause if his faith is not staggered."

By this point, Darwin's opinion of the quinarian system had rather soured, but this did not stop him from sporadically invoking his three-element theory. When Georges Berkeley defended a quaternary arrangement of fungi, Darwin wrote, "**Owing to Plants not being adapted to air!!**"

[16] By this point, Darwin had reconceived the "type" of each group as the current species within the group that had "wandered least" from the ancestral form (B206).

[17] Note that Darwin's parenthetical ("2.typical 3.suptypical") runs together Macleay's division of all groups into two normal and three aberrant subgroups with Swainson's terminology (Swainson divided all groups into one typical, one subtypical, and one aberrant subgroups). At this point, Darwin had not read *Horæ Entomologicæ* (see David Kohn's estimated chronology of the C notebook; Barrett et al. 2008, 737) and was most likely working from his reading of Swainson (B92).

(C95). Later, he wrote, "Insects & birds are the only two tribes fitted for water, air, & land, (Macleay has this remark) / Mem. number 5 here most evident!!? examine into this case" (C218). Thus, while Darwin thoroughly rejected the generality of the quinarian system, he was still willing to allow that in some groups the number five should occur prominently. After C218, the three-element theory dropped silently out of the notebooks. Though Darwin did not, in the notebooks, offer any explicit rejection of it, neither did he invoke it. Later comments make it clear that Darwin had wholly rejected it. On D62, Darwin wrote: "any one may believe anything in such rigmaroles about analogies & number." In 1844, Darwin explicitly rejected his previous attempts to explain the quinarian system via the three-element theory: "It is an hallucination, to suppose that quinarianism can be explained by air, earth & water" (quoted in Ospovat 1981, 113). In the essay of 1844, Darwin (1986, 151) commented:

> […] the number of divisions, such as genera, sub-families, families, &c., &c., has been quite arbitrary; without the clearest definition, how can it be possible to decide whether two groups of species are of equal value, and of what value?

To this passage, he added a footnote connecting this reflection to the quinarian system: "I discuss this because if Quinarism true, I false." Though Darwin did not expand on the exact connection, it appears that he was repeating his charge of C73-74 (quoted earlier in this section) that the arbitrariness of ranking explains why the quinarians found regular numbers in nature. This was the only reference to the quinarian system in that essay.

Adaptation to the three elements does appear in the *Origin* (C. Darwin 1964, 428), but serves there only to explain why naturalists have been misled into finding numerical regularity in organisms. It does not underwrite any real regularity, even of the attenuated sort found in the B notebook.

5.2. Abandoning circularity

Darwin's views about circularity followed a similar arc. In the B notebook, Darwin had offered an explanation of circularity in terms of the bases of branches going extinct. These circles were not proper quinarian circles as they excluded extinct forms, but Darwin was still willing to admit that circular patterns might appear if one looked exclusively at current forms. In the C notebook, Darwin continued to explain circularity in terms of extinction, but further weakened the sort of circularity that could be expected to appear:

> I should think meaning of circular arrangement was only so far true as avoided linear arrangement **the central twigs dying, affinities would be ‹circular› in broken circles.—** which in each group is quite fatal.— Relations of analogy being those last obtained less firmly fixed & therefore most subject to change,—may account for certain organs not being fixed, ‹whi› in some genera which are most fixed in others. (C139)

Darwin here suggested (a) that linear arrangement is hopeless in most groups, (b) that the dying out of "central twigs" yields a circular arrangement, but that (c) these circles are "broken" rather than perfect, and (d) that showing the falsity of linear arrangements was the only true element of circular arrangements.[18] The third point is especially important. The circles that Darwin considered here were haphazard, "broken" circles. They were disorderly and irregular, very far from Macleay's continuous chains of affinity returning into themselves. Darwin continued to advert to this explanation of pseudo-circularity later in the notebooks (C150, D58). By the end of 1843, Darwin

[18] In making this comment, Darwin may also have had in mind the work of George Waterhouse, a non-quinarian circularist.

had completely rejected the reality of circles, writing in a letter to George Waterhouse:

> I believe infinite harm has been done by these circles, which catch the eye as of equal size, & inevitably lead the mind to suppose they are of equal value – it is by this artifice, as I believe, the possibility of making the quinarian system appear probible [*sic*] has chiefly rested. (Darwin to G. R. Waterhouse 3 or 17 December [1843]. Letter 718)

5.3. Osculant groups

Darwin thus increasingly rejected two major elements of the quinarian system in the later species notebooks. At the same time, however, he continued to believe that osculant groups tend to have few species, and further developed his explanation of this fact.

In the C notebook (and in the *Origin*), Darwin frequently did not distinguish between aberrant and osculant groups, and some passages suggest that he took having few species to be definitive of a group being aberrant/osculant. At C87, for instance, Darwin argued that the claim was a truism.[19] At other times, however, Darwin discussed a special class of aberrant/osculant groups, those partially intermediate between two groups, and these are close to Macleay's osculant groups.

The key passages discussing these groups in the notebooks are C201-203. Darwin began by noting that "there can be no animal at present time having an intermediate affinity between two

[19] Macleay (1842, 198), by contrast, explicitly rejected the view that aberrant groups must have relatively few species: "Now this arrangement differs from that of Swainson, in making the vast majority of fishes an aberrant group; but it is the structure, not the number of species it contains, that determines the place of a group in nature."

classes," though a contemporary species can be the "descendent of some intermediate link" (C201). This impossibility of concurrent genuine intermediates is a consequence of Darwin's temporalization of classification (Di Gregorio 1996). Darwin insisted that, even in the presence of such descendants of intermediate links, "the only connection between two such classes will be those of analogy" (C201), that is, contemporary groups do not "pass into each other" (B25). Similarly, "osculant groups between two circles of equal value must be so from characters of analogy" (C202), in contrast to Macleay's insistence that osculant groups connect two other groups by affinity.

Darwin noted that his explanation of why osculant groups tend to have few species (described below) accorded well with an observation Macleay had made: "see my notes on p. 37 of Macleay. wonderfully accordant. with fact there stated, only in most discordant groups" (C202). Darwin was referencing a footnote in *Horæ Entomologicæ*, in which Macleay (1821, 37n) qualified his claim that osculant groups have few species:

> It ought to be observed that this peculiarity is not so remarkable in the genera which connect the two circles of *Petalocera* with each other, and therefore it may perhaps belong solely to those singular insects which serve to connect the more discordant groups.

Darwin's explanation of this fact was based on considerations of the manner in which discrete genera can be formed. Given initial divergence, genera can form if the ancestral species dies out. This can occur if (a) the father-species is "little adapted to some physical change" or (b) there is some such "accident as submersion of land containing all of intermediate Father-species" (C203). Osculant genera result when the elimination of the father-species is imperfect. Because the intermediate species are decimated in some fashion in the formation of genera, "any osculant species

which survived would be few in number.—" Implicit in this is the idea that in more greatly divergent (more "discordant") groups, the decimation of intermediates would be even more drastic, and thus there especially osculant groups would have fewer species.

5.4. Summary

Darwin took, in the C and later notebooks, an increasingly deflationary attitude toward two of the most important patterns that characterize the quinarian system: regularity of number of circularity of groups. At the same time, he offered a mostly non-deflationary explanation for why osculant groups should have few species.

Interestingly, in the majority of the passages on these topics, Darwin made no explicit reference to any particular work by Macleay. On C218, relating to the three-element theory, Darwin mentioned that Macleay had made a relevant remark, but Darwin seems to have been working from memory and not from a fresh reading of Macleay's texts. On D50, Darwin noted, without comment, that Macleay in an 1838 paper (Macleay 1838) still believed that groups were circular. The discussion of why some groups should appear circular on D58 is in close proximity to this note, but Darwin did not there explicitly invoke Macleay. Finally, on C202 (cited above), Darwin attempted to directly explain a phenomenon he found in Macleay's work. C202 is the only time this occurs in the notebooks. The same holds for Darwin's "abstract" of *Horæ Entomologicæ* (Di Gregorio 1996). His notes there concern a wide range of topics, including reproduction, variation, systematic methodology and the affinity/analogy distinction, the nature of osculant groups, the distinction between humans and animals, and vitalism. Discussion of circularity are rare, and discussions of each group having five subgroups are wholly absent.

This pattern is odd, for Darwin, as he was writing the later species notebooks, read several of

Macleay's works *Horae Entomologicæ* (1821), Macleay's letter to Bicheno (1829b), a paper on the genus *Capromys* (1829a), the Fleming-Macleay dispute (Fleming 1829; Macleay 1830a), and Macleay's contribution to Smith's *Illustrations of the Zoology of South Africa* (1838).

Why, if Darwin was actively reading Macleay throughout this period, did his reading figure so rarely in his discussion of quinarian patterns? I suggest that this occurred because Darwin had, by this point, basically rejected, except in severely deflationary form, all of the major patterns the quinarians believed they had discovered. Reading more reiterations of the existence of these patterns probably was uninteresting for Darwin. Darwin did develop a sophisticated explanation of one minor quinarian pattern—the fact that osculant groups tend to have few species—but this was in reaction to a single offhand remark expressing a loose generalization.

So, if Darwin was not much interested in the quinarian system itself, why did Darwin read so much of Macleay's work during this period? What did he find in it to hold his attention?

6. The C, D, and E notebooks: principles waxing

Darwin's interest in quinarian principles may be split into three components. He was interested in (a) Macleay's views on the human/animal distinction, (b) Macleay's views on the nature of species, and (c) Macleay's method of variation. I take these up in turn.

6.1. The throne of reason

Darwin was especially interested in the distinctions between humans and other animals, as he wished to claim that evolutionary processes had produced humans (and in particular the mental faculties of humans), just as they had produced all other organisms. For instance, from C74-79, Darwin reflected on how humans might have evolved, focusing especially on the apparent mental

gap between humans and other animals. Darwin disputed the reality of this gap, arguing that there is gradation in mental powers, just as in bodily features.

When Darwin read the Fleming-Macleay dispute, the gradation of mental powers was among the central issues that captured his interest. After reading Fleming, Darwin wrote, "It will be necessary from manner Fleming treats subject to put in alternative of Man created by distinct miracle" (C156). On the next page, Darwin copied down a quote from Macleay's response: "if she has put man on the throne (*of reason*), she has also placed a series of animals on the steps that lead up to it" (C157).[20] For Macleay, humans, like all other species, were part of the natural system, and thus there must be continuity between them and other animals. While Macleay (1830a, 21) did argue that any discontinuity created by the presence of an immaterial soul in humans and not in other animals was outside the scope of natural history, he explicitly argued for continuity in their mental faculties, as Darwin noted.

To defend the claim that nature is continuous, Macleay had to grapple with the existence of apparent gaps between known groups. To address this issue, Macleay (1830a, 23) distinguished between *hiatus* and *saltus*. A hiatus was a gap or "chasm" in which some steps of a continuous transition can be seen, but in which many steps were as yet unfilled by known species. A hiatus was a sign of ignorance and did not indicate the failure of continuity. A saltus, by contrast, was a genuine leap that violated continuity. After reading the Fleming-Macleay dispute, Darwin began to adopt this language, even in passages where he did not cite Macleay. For instance, on C154, he

[20] The original quote is from Macleay (1830a, 20). The parenthetical is Darwin's addition.

wrote, "Animals have voice so has man. Not saltus but hiatus..."[21] Likewise, at C198, he commended Blyth—"His distinction between reason & instinct very just"—but argued that "these faculties being viewed as replacing each other it is hiatus & not saltus." At C223, again referring to Blyth, Darwin wrote, "I will never allow that because there is a chasm between Man [...] and animals that man has a different origin."[22]

In the M and N notebooks, in which Darwin continued to try to show the continuity between human and animal mental capacities, Macleay is never referenced, but the language of hiatus and saltus does make one appearance, at M151:

> The whole argument of expression more than any other point of structure takes its value. from its connexion with mind, (to show hiatus in mind not saltus between man & Brutes) no one can doubt this connexion.

The language of hiatus and saltus did not persist into *The Descent of Man* or *The Expression of the Emotions in Man and Animals* (C. Darwin 1871a, 1871b, 1872).

Darwin never cited Macleay in *The Descent of Man*, and there are no obvious traces of his influence. However, one passage is worthy of note. In the chapter "On the Affinities and Genealogy of Man," Darwin (1871a, I:186) wrote:

> Spiritual powers cannot be compared or classed by the naturalist; but he may en-

[21] Though C154 occurs before the passages just discussed, Darwin mentions the "Macleay letter to Fleming" on C149.

[22] This interest in the hiatus/saltus distinction also appears in Darwin's abstract of *Horæ Entomologicæ* (Di Gregorio 1996, 111).

> deavor to shew, as I have done, that the mental faculties of man and the lower animals do not differ in kind, although immensely in degree.

There is no evidence that Darwin, writing over three decades after having read Macleay's response to Fleming, had Macleay in mind in writing this. Nevertheless, Darwin's claim here mirrors Macleay's (1830a, 20) position, in which discussion of the soul was excluded from natural history:

> Secondary operative causes [which include human souls, cf. Macleay 1821, p. 179] are no doubt constructed, like forms of matter, also on a wise plan; but if Dr. Fleming wishes to form a Dichotomous System of them, I fear he must patiently wait for his departure from a world which has furnished us only with senses capable of distinguishing the various forms of matter.[23]

Darwin and Macleay thus both attempted to forestall using the human soul or "spiritual powers"

[23] On this point, Macleay is a bit unclear about just what is excluded, because he is unclear what is due to the human soul. The paragraph from which this quote is taken begins, "But, after all, this has really little to do with our present subject, unless the D.D. be a materialist." The reference of "this" is ambiguous. The previous paragraph discusses human and animal mental powers generally (including the "throne of reason" quote Darwin noted), then ends with a discussion of speech as the primary factor creating a gap between humans and ourang-outangs. "This" might refer either to mental powers generally, in which case Macleay differs from Darwin in excluding mind from natural history altogether (despite insisting on continuity between humans and animals in their mental powers). Alternatively, "this" might refer solely to speech as a special function of the soul, added atop the mental powers of animals. In this case, Macleay's position, though not identical with Darwin's, is much closer.

to argue for a discontinuity between humans and animals. Both claim that such matters are outside the scope of natural history. But, to reiterate, I know of no evidence that Macleay influenced Darwin on this point: it seems they simply concurred.

In summary, regarding the issue of the connection between human and animal mental powers, Macleay's work did not substantially change Darwin's position. Macleay and Darwin were simply in agreement on a point that Darwin had arrived at independently of reading Macleay. In reading Macleay's work, Darwin was happy to find an ally, and Macleay appears to have furnished him with a vocabulary by which to think through the animal origins of the human mind, though Darwin's use of this vocabulary persisted for only a few months after he encountered it in Macleay's work.

6.2. Species and varieties

At the back of the C notebook, Darwin made a list of "Books examined: with ref: to Species." Included on this list are "Macleay's letter to D^{r}. Fleming. & review of latter in Quarterly" (C276) and "Macleay's Horæ Entomologica" (C275). As is well known, Darwin in the *Origin* argued that there was no clear-cut distinction between species and varieties. In Macleay, Darwin found a partial ally on this point.

On C42, Darwin praised Macleay (1829b) for his "fine, views about Species." In that paper, Macleay had argued for the difficulty of testing whether a purported species is truly an insulated species, or merely a variety. If a species is "that distinct form originally so created, and producing, by certain laws of generation, others like itself," then a problem arises: one cannot test experimentally whether a form was distinctly created (Macleay 1829b, 405). But this is "clearly the essential characteristic," since some varieties produce offspring like themselves, e.g., human races (Macleay

1829b, 406). In this, we can see (a) that Macleay's views were not identical to Darwin's, as he accepted the distinct creation of species and (b) that Macleay nonetheless held similar views to Darwin on the matter of distinguishing varieties and species in practice.

As in the case of the hiatus-saltus distinction, Darwin's thinking does not appear to have been substantially changed by his encounter with Macleay. He was nonetheless gratified to find another naturalist not only grappling with the same problems that interested him, but arriving at a similar solution to them. On D52, while reflecting on Macleay (1838), Darwin wrote, apparently with considerable excitement, that Macleay "does not know any difference between *permanent variety & species!!*"

6.3. The method of variation

Finally, and most importantly, we must consider Darwin's reaction to Macleay's method of variation.[24] Macleay had argued, in keeping with his belief in the continuity of organic nature, that the appropriate way to classify organisms was not to set up divisions (e.g., bent vs. straight antennae), but rather to trace how animal forms gradually transition into one another.[25] In principle, this method should consider all parts of an organism, since Macleay took organisms to pass into one another on the whole and not just in single parts. Reliance on a single part risked confusing anal-

[24] For primary sources illuminating the method of variation, see Macleay (1821, chap. 1, 1827, 1830a, 32, 1830b). For scholarly treatment, see Novick (2016, 108–10).

[25] In his abstract of *Horæ Entomologicæ*, Darwin explicitly noted the connection Macleay drew between continuity and systematic methodology (Di Gregorio 1996, 113).

ogies for affinities, since analogies were striking resemblances in single features against a backdrop of overall dissimilarity. Thus, only by looking at similarities in the context of the entire organism could affinities be clearly distinguished from analogies.

Nonetheless, Macleay recognized that, in practice, naturalists needed to specialize on particular parts.[26] The idea was to take graduate series of variation in specific parts as imperfect proxies for the overall graded series of variation in organisms. Only such a method could lead to the discovery of the natural system. Reliance on divisions would lead only to an artificial system. In the first part of *Horæ Entomologicæ*, Macleay focused on the mouthparts of scarabs, and he clearly laid out the principles supporting this choice.

Fundamentally, this method requires variation in the structure(s) under consideration between the species being compared (figure 4, rightmost column). However, it can be confounded by sexually dimorphic variation and is thus most readily applicable when members of different sexes of the same species have (a) the same number of a particular part and (b) do not differ in the structure of that part (figure 4, second and third columns). The method can also be confounded by variation in number of a particular part among the species being compared (figure 4, fourth column). The idea is that equal numbers of parts are required to set up clear correspondences, to know precisely which parts should be fit into the overall series. The ideal part for use in classification is thus invariable as to number and form in the sexes, invariable as to number in the species, and variable as to form in the species (figure 4). Applying this to his own work, Macleay selected the maxillae and the mentum for use in classifying the scarabs (the oculi were too small to be practical).

[26] See Lowther (2016, 17–18) for discussion of debates over the proper characters to use in classification.

Of crucial importance to this method is that the most useful characters will vary by group. For instance, Macleay (1821, 4) stressed that his table of variation (figure 4) was "to be considered with reference to the Coleopterous insects only." The ideal character for any group will be assimilable to "one general plan of construction," yet will also be "subject in detail to all those endless changes of form" that result from being made to serve different functions (Macleay 1821, 2). Thus, though useful characters would differ by group, Macleay (1830a, 32) could provide guidelines to "prevent the selecting such systems of organs at hazard." Macleay (1830a, 32) suggested the general rule that the value of a character "ought to rise in importance only in inverse proportion to its degree of variation" within that group.

It is not hard to see why Darwin, who was himself an accomplished systematist and who was in the process of developing a temporalized understanding of continuity in organic nature (Di Gregorio 1996), would have been interested in and sympathetic to Macleay's method. Indeed, Darwin frequently discussed it while reading Macleay's work. The issue first appears in Darwin's notebooks when he read the Fleming-Macleay dispute. Cutting out, for the moment, Darwin's later additions to the entry, Darwin wrote:

> Where any structure is general in all species in group we may suppose it is oldest, & therefore lest subject to variation.— now some such «characters» rule are used by Naturalists in their test of value of character— Therefore value of organs vary in different group. & Not known in single ones—. viz. Macleay letter to Fleming p. 32… (C149)

In this passage, Darwin tried to explain one aspect of Macleay's method of variation: that characters are useful in inverse proportion to their degree of variation. Darwin argued that the oldest characters tend to vary least, and thus that the amount of variation in a part can be a guide

to genealogical relationships. In a later addition to this page, however, he wrote, "**Macleys rule is converse, ‹when› value of character depends on non-variation, & not on extension ?these go together?**" Here, Darwin drew a distinction between *non-variation* (the subject of Macleay's rule) and *extension*. The former concerns the degree to which a part varies, in those species in which it is present. The latter concerns how widely it is distributed. He tentatively suggested that the two might coincide, as would be expected if the oldest characters (which would have the widest extensions) varied least.

On C202, Darwin returned to the theme (cf. C158): "Characters of analogy.—last acquired,— or aberrant, therefore more easily modified... WHERE CHARACTER VARIABLE it is (one of analogy or) LATELY ACQUIRED." Though he did not cite Macleay on this point, the passage occurs in the midst of a discussion of osculant groups in which Darwin did cite Macleay (see above, §5.3). This passage shows Darwin connecting his reflection on the method of variation and the variable worth of characters to his attempt to understand relations of analogy in an evolutionary framework.

Darwin's interest in the method of variation persisted into the D and E notebooks. From D50-53, Darwin reflected upon his reading of Macleay (1838). Darwin again offered the explanation developed at C149: "Macleays plan of arrangement depends on the organs judged to be of importance in inverse ratio to their variability.— (Now cæteris paribus these will be the oldest)" (D50). From this we can see that, even very late in his explicit engagement with Macleay, Darwin took Macleay as "more or less right"—only now at the level of methodology. The same holds true of the passage at E22 where, apparently responding to something he heard Macleay say in person, Darwin wrote: "Macleay says that ‹every› «any» character even colour is *good*. (ie invariable) in some classes— it is because every part is under change, now one part now another."

6.4. Summary

Darwin's explicit engagement with Macleay's written work began in the C notebook. By this time, Darwin had almost entirely rejected the reality of the patterns the quinarians had found in nature. Insofar as he did accept them, he did so only in an extremely attenuated form. Yet Darwin during this period read several of Macleay's most important works. Why did he read them? There is little evidence that he did so in order to firm up his rejection of quinarian patterns, for explicit references to particular texts rarely occur in the passages where this rejection is articulated. Rather, Darwin took an interest in Macleay's works because he found himself in sympathy with Macleay's more abstract views on the nature of species, on the human/animal distinction, and, especially, on the means of determining which characters were useful for classification. As Di Gregorio (1996, 114) noted regarding Darwin's abstract of *Horæ Entomologicæ*, Darwin "plundered" Macleay's work "of all its riches" and reorganized Macleay's ideas "under entirely new headings." What's crucial to note is the nature of those riches: they concerned the background commitments informing Macleay's system, not the system itself. Importantly, these were elements of Macleay's work that Darwin could only get from Macleay's texts (or from Macleay himself), and not from second-hand representations of Macleay's works, which (a) focused on quinarian patterns and neglected these underlying principles and (b) centered around Vigors' and Swainson's variants on the quinarian system, as Lowther (2016) has argued.

7. Quinarian traces in the *Origin*

Did Darwin's engagement with the work of Macleay have any lasting effects, and in particular any effects on the *Origin*? This question has received scant discussion. Ospovat (1981, 113) does

discuss Darwin's relation to Macleay's ideas up to the *Origin*, but suggests that Darwin at that point was merely thinking about whether or not he needed to discuss Macleay at all: "But when he mentioned [the quinarian system] in the *Origin*, it was to show how naturalists had been misled into developing the quinary and other similar systems." This account is correct as far as it goes, but it concerns only quinarian patterns.

At first glance, Ospovat's account appears to capture the entire role that Macleay's work played in the *Origin*. Darwin (1964, 427) praised Macleay for his role in distinguishing affinity from analogy, but on the next page explained how the quinarians deceived themselves, using the same argument found at C73-74.[27] Ospovat (1981, 178) also correctly notes the connection between Macleay's work and Darwin's explanation of why osculant groups have few species, linking this explanation to Darwin's principle of divergence, which plays such a prominent role in the *Origin*. In that way, Ospovat has suggested that Darwin's engagement with Macleay made a contribution to the *Origin* beyond simply serving as a bogey to be rejected.

In addition to this, however, Darwin's reflections on the method of variation also made a contribution to Darwin's discussion of classification in chapter 13 of the *Origin*. Recall that Darwin, in attempting to think through "Macleys rule" (C149), had drawn a distinction between a character (a) showing little variation and (b) showing wide extension. Darwin had at first assimilated the two, only later realizing that Macleay's method only required lack of variation, while wide extension was something distinct.

[27] Interestingly, Darwin assimilated Macleay's affinity/analogy distinction to a similar distinction in Lamarck, despite having commented on a passage in which Macleay (1830a, 24) explicitly rejected that assimilation (C158).

This distinction persisted into the *Origin*: "If [taxonomists] find a character nearly uniform [i.e., showing low variation], and common to a great number of forms [i.e., showing wide extension], and not common to others, they use it as one of high value" (C. Darwin 1964, 418). Darwin speculated in the notebooks that these would generally co-occur, and in this passage he treated them together. In principle, however, they could come apart, and Darwin elsewhere separated them. Thus the discussion of Marshall on cattle horns (C. Darwin 1964, 423) focused exclusively on low variation, while the discussion of why "we care not how trifling a character may be" (C. Darwin 1964, 425–26) mentioned only wide extension. In these passages, we see both that Darwin still accepted "Macleys rule" as he understood it, albeit without using that name, and that he preserved the distinction between this rule and the distinct rule concerning the extension of characters.

From this we see that while Darwin's explicit engagement with the work of Macleay was primarily concentrated within a brief window (the time in which Darwin maintained the species notebooks), the influence of this engagement did not end with Darwin's nearly wholesale rejection of the quinarian system in the C notebook. It made a lasting contribution to Darwin's understanding of the methodology of classification. It thereby made a lasting contribution to his evolutionary theory, and to the book that first presented it.

8. Conclusion

I have here argued that Darwin's engagement with Macleay was richer than has hitherto been noticed. Darwin did not just try to explain quinarian patterns. Rather, when he read Macleay's work, he took a substantially greater interest in the principles underlying this work, finding himself sympathetic to many of them. Specifically, he sympathized with Macleay's views on the distinc-

tion between human and animal minds, the distinction between species and varieties, and the methodology of classification. This interest arose at the same time that Darwin became increasingly pessimistic about the reality (in however attenuated a form) of the majority of quinarian patterns. I have also suggested that the influence of this engagement on the *Origin* extends beyond the two pages (C. Darwin 1964, 427–28) in which Darwin explicitly mentioned Macleay's work. In the course of reading Macleay's work, Darwin for the first time came to draw a distinction between two properties relevant to assessing the taxonomic value of characters: the degree to which they vary, and the extent to which they characterize a particular group in contrast to others.

Works cited

Barrett, Paul H., Peter Jack Gautrey, Sandra Herbert, David Kohn, and Sydney Smith, eds. 2008. *Charles Darwin's Notebooks, 1836-1844*. Cambridge: Cambridge University Press.

Darwin, Charles. 1871a. *The Descent of Man, and Selection in Relation to Sex*. Vol. I. London: John Murray. http://darwin-online.org.uk/content/frame-set?itemID=F937.1&viewtype=text&pageseq=1.

———. 1871b. *The Descent of Man, and Selection in Relation to Sex*. Vol. II. London: John Murray. http://darwin-online.org.uk/content/frameset?itemID=F937.2&viewtype=text&pag-eseq=1.

———. 1872. *The Expression of the Emotions in Man and Animals*. London: John Murray. http://darwin-online.org.uk/content/frameset?itemID=F1142&viewtype=text&pageseq=1.

———. 1964. *On the Origin of Species*. Edited by Ernst Mayr. Facsimile. Cambridge, MA: Harvard University Press.

———. 1986. *The Foundations of the Origin of Species: Two Essays Written in 1842 and 1844*. Edited by Francis Darwin, Paul H. Barrett, and R. B. Freeman. New York: NYU Press.

De Beer, Gavin. 1963. *Charles Darwin: Evolution by Natural Selection*. Garden City, NY: Doubleday and Company.

Di Gregorio, Mario A.. 1996. "The Uniqueness of Charles Darwin: His Reading of W.S. Macleay's Horae Entomologicae." *Historical Records of Australian Science* 11 (2): 103–17. https://doi.org/10.1071/HR9961120103.

Fleming, John. 1829. "On Systems and Methods in Natural History. By J.E. Bicheno, Esq. 1829. (Linn. Trans., Xv, Part 2.)." *Quarterly Review* 41: 302–27.

Ghiselin, Michael T. 1969. *The Triumph of the Darwinian Method*. Berkeley: University of California Press.

———. 2004. "Mayr and Bock versus Darwin on Genealogical Classification." *Journal of Zoological Systematics and Evolutionary Research* 42 (2): 165–69. https://doi.org/10.1111/j.1439-0469.2004.00258.x.

Gray, John E. 1824a. "On the Arrangement of the Papilionidae." *Annals of Philosophy* NS 8: 119–20.

———. 1824b. "On the Natural Arrangement of the Pulmonobranchous Mollusca." *Annals of Philosophy* NS 8: 107–9.

———. 1825a. "A Synopsis of the Genera of Reptiles and Amphibia, with a Description of Some New Species." *Annals of Philosophy* NS 10: 193–217.

———. 1825b. "An Attempt to Divide the Echinida, or Sea Eggs, into Natural Families." *Annals of Philosophy* NS 10: 423–31.

———. 1825c. "An Outline of an Attempt at the Disposition of Mammalia into Tribes and Families, with a List of the Genera Apparently Appertaining to Each Tribe." *Annals of Philosophy* NS 10: 337–44.

Hodge, Jonathan. 2013. "The Origins of the Origin: Darwin's First Thoughts About the Tree of Life and Natural Selection, 1837-1839." In *The Cambridge Encyclopedia of Darwin and Evolutionary Thought*, edited by Michael Ruse, 64–71. Cambridge: Cambridge University Press.

Jenyns, Leonard. 1835. "Report on the Recent Progress and Present State of Zoology." *Report of the British Association for the Advancement of Science* 4: 143–251.

Lowther, David. 2016. "The Reverent Eye: Scientific Visual Culture and The Origins of Modern

British Zoology, 1815-1840." Newcastle University.

Macleay, William Sharp. 1821. *Horae Entomologicae: Or Essays on the Annulose Animals*. London: S. Bagster.

———. 1827. "On the Structure of the Tarsus in the Tetramerous and Trimerous Coleoptera of the French Entomologists." *Transactions of the Linnean Society of London* 15 (1). Blackwell Publishing Ltd: 63–73. https://doi.org/10.1111/j.1095-8339.1826.tb00108.x.

———. 1829a. "Notes on the Genus *Capromys* of Desmarest." *The Zoological Journal* 4: 269–78.

———. 1829b. "A Letter to J. E. Bicheno, Esq., F.R.S., in Examination of His Paper 'On Systems and Methods' in the Linnean Transactions." *Philosophical Magazine* Series 2 6:33. Taylor & Francis Group: 199–212. https://doi.org/10.1080/14786442908675120.

———. 1830a. *A Letter on the Dying Struggle of the Dichotomous System*. London: Richard Taylor.

———. 1830b. "Explanation of the Comparative Anatomy of the Thorax in Winged Insects, with a Review of the Present State of the Nomenclature of Its Parts." *The Zoological Journal* 5: 145–79.

———. 1838. *Illustrations of the Annulosa of South Africa: Being a Portion of the Objects of Natural History, Chiefly Collected During an Expedition into the Interior of South Africa, Under the Direction of Dr. Andrew Smith, in the Years 1834, 1835, and 1836, Fitted*. London: Smith, Elder.

———. 1840. "Observations on Trilobites, Founded on a Comparison of Their Structure with That of Living Crustacea." *Annals and Magazine of Natural History* 4 (21): 16–22. https://doi.org/10.1080/00222934009512445.

———. 1842. “On the Natural Arrangement of Fishes.” *Annals and Magazine of Natural History* 9 (57): 197–207. https://doi.org/10.1080/03745484209445326.

McMillan, Nora F., and Walter O. Cernohorsky. 1979. “William Swainson, F.R.S., in New Zealand with Notes on His Drawings Held in New Zealand.” *Journal of the Society for the Bibliography of Natural History* 9 (2): 161–69. https://doi.org/10.3366/jsbnh.1979.9.2.161.

Montagu, George. 1831. *Ornithological Dictionary of British Birds*. Edited by James Rennie. 2nd ed. London: Hurst, Chance and Co.

Novick, Aaron. 2016. “On the Origins of the Quinarian System of Classification.” *Journal of the History of Biology* 49 (1): 95–133. https://doi.org/10.1007/s10739-015-9419-2.

Ospovat, Dov. 1981. *The Development of Darwin’s Theory: Natural History, Natural Theology, and Natural Selection, 1838–1859*. Cambridge: Cambridge University Press.

Reider, William D. 1841. *The New Tablet of Memory; or, Recorder of Remarkable Events, Compiled, and Alphabetically Arranged from the Earliest Period to the Present Time*. London: John Clements.

Swainson, William. 1835. *A Treatise on the Geography and Classification of Animals*. London: Longman, Rees, Orme, Brown, Green & Longman.

Figures

Figure 1 Macleay's (1821, 25) arrangement of *Scarabæus*. Recreated in Photoshop by Michal De-Medonsa. Reprinted from (Novick 2016)

Figure 2 Macleay's (1821, 318) arrangement of Animalia. Recreated in Photoshop by Michal De-Medonsa. Reprinted from (Novick 2016)

Figure 3 Model of the three-element theory applied to the case of adaptation to three elements (left) and two elements (right). Abbreviations: Te (terrestrial), Ae (aerial), Aq (aquatic), referring the primary element inhabited by a group. Further explanation in text. Created using Adobe illustrator

Figure 4 Macleay's (1821, 4) table of variation in the coleopterous insects. Recreated in Photoshop by Michal De-Medonsa. Reprinted from (Novick 2016)

Conflict of interest: The author declares that they have no conflict of interest.