Charles Darwin's Zoology Notes & Specimen Lists from H.M.S. Beagle

This transcription of notes made by Charles Darwin during the voyage of H.M.S. Beagle records his observations on the animals and plants that he encountered, and provides a valuable insight into the intellectual development of one of our most influential scientists. Darwin drew on many of these notes for his well known Journal of Researches (1839), but the great majority have remained unpublished. The volume provides numerous examples of his unimpeachable accuracy in describing the wide range of animals seen in the course of his travels, and of his closely analytical approach towards every one of his observations. Only at the very end of the voyage were his first doubts about the immutability of species consciously expressed, but here are to be found the initial seeds of his theory of evolution, and of the fields of behavioural and ecological study of which he was one of the founding fathers.

CHARLES DARWIN'S ZOOLOGY NOTES & SPECIMEN LISTS FROM H.M.S. *BEAGLE*

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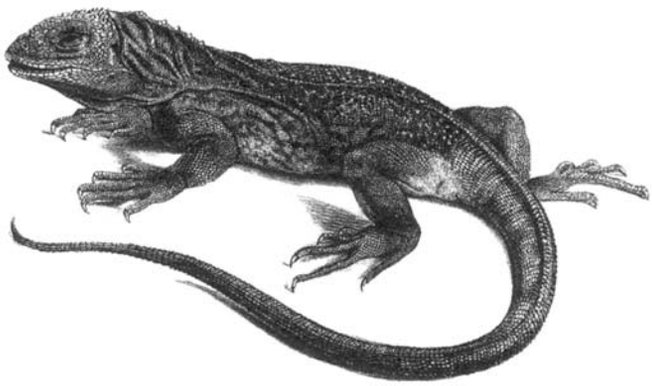

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To

CHARLES ROBERT DARWIN

whose dedication and skill as an observer
of Nature has set an example for all time

Contents

Introduction

Charles Darwin, referred to hereafter as CD, arrived in Plymouth on 24 October 1831 in order to accompany Captain Robert FitzRoy on H.M.S. *Beagle* as a scientist and companion. As he noted in his private journal[1], the ship was 'in a state of bustle and confusion'. The carpenters were hard at work fitting up the drawers in the poop cabin, but the corner assigned to him, where for the next five years he was destined to work at his microscope and write his notes, looked too small to accommodate all his possessions[2]. A month later he was able to carry his books and instruments on board, and soon his fears about lack of space had been dissipated. On 4 December he mastered the technique of getting into his hammock, and slept on board for the first time. There followed an endless succession of southwesterly gales that kept the *Beagle* at anchor, and forced the abandonment of two attempts to sail, until on 27 December the wind shifted to the east, and the ship at last got under way.

Although CD's most important achievements were ultimately in the realm of biology, it must not be forgotten that FitzRoy's original intention was that his scientist should examine the land while the officers of the *Beagle* looked after the hydrography[3]. Shortly after the return of the ship to England in 1836, the Captain duly reported[4] that 'Mr Charles Darwin will make known the results of his five years' voluntary seclusion and disinterested exertions in the cause of science. Geology has been his principal pursuit'. The total bulk of CD's *Geology Notes*[5] was nearly four times greater than that of the *Zoology Notes* transcribed here, and a very rough analysis of the scientific topics covered in his letters to Henslow[6] from the *Beagle* shows that about three times more space was devoted to geology and palaeontology than to natural history. CD's geological findings were duly reported to the Geological Society, of which he had just been elected one of the two secretaries, on 7 March 1838[7,59]. His contribution forming Volume III of the joint account of the voyage edited by FitzRoy that appeared in 1839[8] was entitled simply *Journal and Remarks. 1832-1836.*, and when it was reprinted on its own later that same year it became *Journal of researches into the geology and natural history of the various countries visited by H.M.S. Beagle...*[9] In the second and final edition published in 1845[10], the order in the title was changed to 'natural history and geology', and there it remained. Of his three geological books[11], *Coral reefs* was published in 1842, *Volcanic islands* in 1844, and *Geological observations on South America* in 1846, their writing having occupied four and a half years' steady work[12].

Depending on the opportunities offered to him at different periods, the strength of CD's relative liking for geology and natural history fluctuated, but generally geology came out on top. To his sister Catherine he wrote in April 1834[13] 'there is nothing like geology; the pleasure of the first days partridge shooting or first days hunting cannot be compared to finding a fine group of fossil bones, which tell their story of former times with almost a living tongue'; and to his cousin W.D. Fox he had admitted a year earlier[14] 'The pleasure of working with the Microscope ranks second to geology'. The reason was perhaps, as he put it in his *Autobiography*[15], that in comparison with natural history, 'the investigation of the geology of all the places visited was far more important, as reasoning here comes into play'. And it was indeed more in geology than in natural history that he was able to indulge his latent passion for theorising[16], as became apparent as soon as he landed at St Jago in the Cape Verde Islands on 16 January 1832[5,17].

Nevertheless, he was quickly acting in many of his *Zoology Notes* on the strongly felt principle often quoted later on by Emma Darwin[18]: 'it is a fatal fault to reason whilst observing, though so necessary beforehand and so useful afterwards'; while to Wallace he wrote in 1857[19] 'I am a firm believer that, without speculation there is no good & original observation'. Although at the end of his life he wrote somewhat misleadingly in his *Autobiography*[20] that 'My first note-book was opened in July 1837. I worked on true Baconian principles, and without any theory collected facts on a wholesale scale', the truth was otherwise. While dissecting specimens under his microscope, he was constantly questioning himself about the logical implications of his findings, and his interpretations of their complex internal anatomy were always very closely reasoned. Often he carried out little experiments to test the response of his specimens to mechanical stimulation, or exposure to water of the wrong salinity or to alcohol. Moreover, the entries describing the animals that he watched and sometimes captured in the field were models of critical observation, packed with well thought out comments on the possible reasons for their behaviour, distribution and relation with their environment. He was always ready to question the correctness of the conclusions of his predecessors if they conflicted with what he saw for himself, and his intensely analytical approach was from the beginning one of the characteristics that stands out most clearly in his scientific writing.

The first observation in his *Zoology Notes*, dated 6 January 1832, was concerned with luminous matter in the sea. His collecting began in earnest on 10 January, when having quickly constructed the plankton net of which he drew a sketch[21], 'it brought up a mass of small animals, & tomorrow I look forward to a greater harvest'. The captures described in his notes were some medusae, including a Portuguese man-of-war whose powerful toxin he inadvertently got on to his fingers and into his mouth; some salps; and 'a very simple animal' that was new to him, and remained unclassified until he returned to England. Specimen No. 1 in Spirits of Wine was listed as chiefly pteropods, *i.e.* shelled opisthobranch molluscs such as *Limacina* and *Creseis*. Specimen No. 1 not in Spirits was a cuttlefish extracted from the stomach of a black-backed gull on 6 January, followed by a locust (*Acrydium*) and other insects taken on board the ship during the next few days.

CD's note-taking was distinguished from the very start by its orderliness, and by the manner in which he adhered faithfully to his chosen layouts throughout the voyage. Both for his private journal and for the *Zoology Notes* he wrote in ink on gatherings of paper making pages 20 by 25 cm in size, faintly lined and with a red marginal line[22]. At the head of each page, its number and the month, year and location of the observations were entered. In the *Beagle Diary*, the margin was used only to record the day of the month, and occasionally the day of the week. In the *Zoology Notes* CD quickly settled down after the first few pages to writing in the margin an underlined generic or family name for the specimen under consideration, together with its number and sometimes a further brief description. He soon found himself needing often to add extra notes on the backs of the pages, identified by letters in brackets placed opposite the relevant part of the text. Sometimes these were immediate afterthoughts, and sometimes comments arising later from subsequent observations.

As he had begun, so he continued, and in the end well over half of the pages of the *Zoology Notes* were concerned with marine invertebrates. His concentration on this particular field may be attributed not so much to his admitted pleasure in working with his microscope, but to the fact that during the long periods when the *Beagle* was at sea few other activities

were open to him. It should also be appreciated that the dissection of a single bryozoan or crab sometimes generated half a dozen pages of notes, whereas observations on a beetle or a frog or a bird seldom occupied more than a few sentences. Many years afterwards he wrote[23] that 'from not being able to draw and from not having sufficient anatomical knowledge a great pile of MS. which I made during the voyage has proved almost useless', a typically self-deprecatory judgement on the merits of his *Geology* and *Zoology Notes* that was quoted almost word for word by Thomas Huxley in his obituary of CD for the Royal Society[24]. There were, nevertheless, many splendid descriptive passages drawn from the *Zoology Notes* that provided the natural history in the *Journal of Researches*, and although the results of his anatomical studies on bryozoans, crustaceans and other invertebrates mostly remained unpublished, there were among them, as will be seen, many pioneering observations of considerable interest. CD's modesty about his skill as an artist was borne out, as Huxley confirmed, by the crudity of the sketches that he drew in the *Beagle Diary* and in his letters, so that it comes as a surprise to see the accuracy of the drawings in fine pencil or ink on separate sheets of unlined paper, of the specimens that he subjected to close examination under his single lens Bancks microscope[25], not infrequently showing new and previously unrecognised anatomical features. These formed the 20 Plates preserved in CUL MS DAR 29 and reproduced in this volume, which each comprise up to a dozen Figures. His cross referencing to further mention of an animal on another page of the *Notes*, or to the Plate and Figure illustrating a particular point in the text, was always impeccable. The efficiency with which he thus organised his written records under very cramped conditions in a ship at sea, often stricken by seasickness, was without doubt an extremely important factor in his success as an observer and a collector both in geology and in natural history.

Another striking feature of the *Zoology Notes* is their total professionalism, despite the fact that on the face of it CD had had little appropriate training. However, in company first with his brother Erasmus and then more importantly with Robert Grant[26], he had in 1827 explored the shores of the Firth of Forth as described in an early diary[27], illustrated with forerunners of his sketches in the *Zoology Notes*; and he had received valuable instruction from Grant on the marine invertebrates that were found there. When he then encountered in the open Atlantic a range of organisms with which he was unfamiliar, he at once began to make extremely effective use of the *Beagle*'s quite extensive library of reference books. They were chiefly the works of the notable French encyclopédistes, of which his favourite was what he called *Dic. Class.*, the 17 volumes of the 'Dictionnaire Classique d'histoire naturelle', but he also consulted Cuvier's 'Le règne animale', Lamarck's 'Histoire naturelle des animaux sans vertèbres', Lamouroux's 'Exposition méthodique des genres de l'ordre des polypiers', Rang's 'Manuel de l'histoire naturelle des mollusques et leurs coquilles', and others[28]. With their help he was able to give generic or family names to quite a number of the marine invertebrates that he collected, though not many of them are still in use today, and he ran into difficulties with organisms belonging to phyla whose existence had yet to be recognised. Thus it was ironic that the 'very simple animal' which he caught in his net on 11 January 1832, and of which his drawing in Figure 1 of Plate 1 (see p. 4 of this volume) is instantly recognisable today as a chaetognath or arrow worm[29], still had him 'at a loss where to rank it amongst other animals' when he found large numbers off the coast of Patagonia (see pp. 66-9), and was only identified after his return to England four years later. In 1832 he had

5 1832 St Jago 5

Jan 28th Found amongst the rocks. West of Juan Fernandez Island at low water an Octopus. – When
Octopus first discovered he was in a hole. & it was difficult to perceive what it was. –
As soon as I drove him from his den he shot with great rapidity across the pool of water. – leaving in his train a large quantity of the ink. – even the
when in shallow place it was difficult to catch him. for he twisted his body with great ease between the stones. & by his suckers stuck very fast to them. – When in the water the animal was of a brownish purple. but immediately when on the beach the colour changed to a yellowish green. – When I had the animal in a basin of salt water on board – this fact was explained. by its having the Chameleon like power of changing the colour of its body. – The general colour of animal was French grey with numerous spots of bright yellow. – the former of the colours varied in intensity. – the other entirely disappeared & then again returned. – Over the whole body there were conspicuous chocolate clouds varying in colour from a "pigeon red" to a "chestnut brown". – As seen in a lens. these clouds consisted of minute points. apparently injected with a coloured fluid. the whole animal presented a most extraordinary mottled appearance. & much surp

A typical page from CD's *Zoology Notes*

been unaware of the foundation of the genus *Sagitta* by Quoy and Gaimard some five years previously, and he made up for it in a short note published in 1844[30] that he hoped would 'aid more competent judges than myself in ascertaining its true affinities.' But although the 100 species of Chaetognatha are common among marine plankton in tropical seas, even now the precise relationship of the phylum with the other pseudo-coelomates has not been finally settled.

It may also be noted that the barnacles collected by CD on the *Beagle* — eventually the subjects of his monograph on the Cirripedia[31] written at Down House — were always listed among the molluscs as shells, where they were still placed by Cuvier and Lamarck before J. Vaughan Thompson's discovery[32] in 1830 of their metamorphoses suggested their transfer to the crustaceans. But when CD was examining a shell that at first he had doubtfully entered as the marine snail *Conus* (see p. 135), he decided that because of its strikingly crustacean characteristics and possession of an external 'pied machoire' it was better identified as a barnacle common in the Falkland Islands. Hence independently of Thompson he had already observed the crustacean affinities of barnacles, and as he recognized later[23], a knowledge of crustaceans and of their larval stage the Zoea, was one of the most valuable outcomes of his dissections of marine invertebrates during the voyage.

The principal problem in classification encountered by CD in the 1830s lay in determining the true nature of some of the colonial plant-like invertebrates then still known colloquially as Zoophytes or Polypes, and nowadays separated into Cnidaria such as hydrozoa, anthozoa (including corals) and scyphozoa, Bryozoa and sponges. The smallest of these were the corallines, but thanks to the classical studies of John Ellis[33] it had been accepted in many quarters by the end of the 18th century that like some of the coelenterates closely similar to them in appearance, they belonged to the animal kingdom. Only Linnaeus was not wholly convinced, and coined the name Zoophyta — a group intermediate between plants and animals — for the corallines. In 1820 de Blainville discovered that the polyps of certain zoophytes possessed both mouth and anus, suggesting that they should be placed on a higher level than other coelenterates; and in 1827 Robert Grant[34] observed that some of them had ciliated tentacles and a recurved alimentary canal. In 1830, J. Vaughan Thompson, working independently on zoophytes off the southern shores of Ireland, also discovered that there were two anatomical forms of polyps, and added to his memoirs on crustaceans a fifth entitled *On Polyzoa, a new animal discovered as an inhabitant of some Zoophites*[35], in which he created a new animal class, the Polyzoa, to replace the Zoophyta. As has been explained by Ryland[36], the phylum concerned is now best known as the Bryozoa, while those animals in which the anus opens inside the circlet of tentacles belong to the phylum Entoprocta.

At the beginning of the voyage, CD referred to all such animals indiscriminately as corallines or coralls, although some of them were in fact hydrozoa or hydrocorals, some bryozoans, and some coralline algae. When in the end he had concluded[43] that his 'true corallinas' were indeed algae such as *Corallina* and *Amphiroa*, he listed this group as Nulliporae. The bryozoans were generally 'encrusting corallines' or Flustrae, and the reef-building hydrocorals were Madrepores. He had thus improved on the still prevailing confusion in the classification of the Zoophytes or Polypiferous Polypi in the accounts of Cuvier and Griffith[37] that he had with him on the *Beagle*.

The first corallines to be collected during the voyage were identified as *Sertularia*, a term applicable at that time both to bryozoans and hydrozoans, and a coralline alga *Amphiroa*.

Then in August 1832, off the coast of Patagonia at a depth of 14 fathoms, the first bryozoans were found, a 'corall' listed as 'Cellepora ?' and confirmed in 1901[38] as being *Cellepora eatonensis*, and a specimen which CD immediately and correctly recognised as related to *Flustra*, to whose leaf-like colonies in the Firth of Forth[27] he had been introduced by Robert Grant[26], and with which his first scientific paper, delivered to the Plinian Society in March 1827, had been concerned. But what, seen under his microscope, rendered the new genus 'singular' (see p. 73) was the occurrence of peculiar organs on the edges of the cells that resembled in shape the open beak of a vulture, and nodded continuously at a frequency of about five seconds. He asked himself what their function could possibly be, rejecting generation 'which is the last resource in all puzzling cases'. Later he found similar organs on other zoophytes, and speculated at some length on their role[39]. The organ in question was the type of anascan heterozooid now known as a pedunculate avicularium, and although a defensive role with adaptive value has been proposed for it, even today there is a shortage of firm evidence in support of this or any other hypothesis[40]

More 'coralls', identified by CD from Lamouroux's pictures[41] as *Celleporaria* and other bryozoans now placed in suborder Ascophora, were collected in Tierra del Fuego four months later, while in March 1833 a number of coralline algae were collected around East Falkland Island. Then at Port Desire in January 1834 considerable quantities of the 'Corallina' *Halimeda* were thrown up on the beach, and (see note (b) on p. 187) CD concluded from his examination of their articulation and mode of propagation that 'I do not believe Corallina to have any connection with the family of zoophites'. For as he wrote later to Henslow[42]: 'the 'gemmule' of a Halimeda contained several articulations united, & ready to burst their envelope & become attached to some basis [*i.e.* base]. I believe in Zoophites, universally the gemmule produces a single Polypus, which afterwards or at the same time grows with its cell or single articulation'. It followed that the zoophytes were definitely not plants, although this evidence was provided by the green alga *Halimeda* belonging to the Chlorophyta, and not by the coralline algae belonging to the Rhodophyta[43].

In March 1834, when the *Beagle* was once again in Tierra del Fuego, more specimens of *Flustra* were obtained that were bryozoans of several families of the order Cyclostomata as well as Cheilostomata. Pursuing a 'lately determined' intention, described in July to his sister Catherine[44], 'to work chiefly amongst the Zoophites or Coralls', CD engaged on an orgy of comparative anatomy, and anticipated a remarkable amount of bryozoan biology that had yet to be formally elucidated. He observed in Specimen 874 (see p. 195) the functioning of the autozooidal operculum 'like lower jaw of a bull-dog'. He correctly appreciated (see pp. 197 and 207) the phenomenon of degeneration and regeneration of the bryozoan polypide, and clearly saw the associated brown bodies[36]. He perceived (see p. 197) the relationship between the pedunculate vulture's-head avicularia of the erect species, and the adventitious sessile avicularia of an encrusting form. He observed (see pp. 198 and 206-207) ovicells brooding young, and (on p. 205) described the kenozooidal rootlets (rhizoids) that support and attach many erect forms. Bringing up in his net a specimen of a similar but new animal that he labelled 'polype?' (see pp. 199-201), he at once appreciated the different location of its anus that now distinguishes the phylum Entoprocta.

During the next months, off the coast of Patagonia and further to the south, he collected more bryozoans and accurately described (see pp. 222-3) the anatomy of the ascophoran *Eschara gigantea* with its calcified frontal wall. A few days later (see pp. 226-9) he found

another specimen that he misidentified as the cyclostome *Crisia*, but which was in fact the anascan *Caberea minima*, belonging to the superfamily Cellularioidea. This species possessed the type of heterozooid now known as a vibraculum, a long tapering bristle-like seta mounted on a basal chamber containing musculature capable of swivelling and rotating the seta. CD's graphic description of the coordinated sweeping movements of the setae on each branch of the coralline was a triumph of accurate observation. Again he speculated on the function of the vibracula, and concluded that their role was not 'to drive away enemies and impurities', though the modern view[36] is rather that the species with well developed vibracula depend on their ability to discourage small organisms such as larvae, and particles of sand or silt, from settling on the surface of the colony.

Then at Port Famine in June 1834 he turned his attention (see p. 232) to specimen 983 in spirits of 'a very simple *Flustra*' — which was subsequently identified by S.F. Harmer[38] as belonging to the related species *Membranipora membranacea* — 'so that I might erect at some future day, my imperfect notions concerning the organization of the whole family of Dr Grant's Paper[34]'; and gave a good description of the organisation of its polypus. But this turned out to be the last bryozoan to be discussed in the *Zoology Notes*, and except for quite a number of specimens collected in January 1835 in the Chonos Archipelago and off Chiloe, and two hauls in the Galapagos Islands in September 1835, no more were collected during the second half of the voyage, though further specimens were taken of the coralline algae described by CD as corallinas, and of the true reef-building hydrocorals.

Nevertheless, CD's resolution to think further about the organization of the Flustrae was not wholly abandoned. It has survived, at least in part, as two loose pages of conclusions about the anatomy of corallines, probably written on board the *Beagle* early in 1836, to which attention was drawn by Sloan[45]. Here CD has in effect decided that the Flustraceae belong in a phylum of their own, although nowhere did he ever refer to Ellis[33] or Thompson[35], and is musing constructively on their biology. These two pages are listed as CUL MS DAR 5.98-9, the page numbering being that of the cataloguer, not CD's, and run as follows:

> [p. 98 commences]
> That the number of arms in Polypus of the Flustraceæ varies from 8 to 28 & is no more than a Specific character:
> That a proportion is kept up between simplicity of Polypier & number of arms.— that the same essential organ[s] are found in very varying forms of Polypier.—
> That the degree of stony nature in Corallines is entirely futile as a character[46].—
> That the ~~fo~~ orders of Lamouroux of Cellepora.— Cellaria & Flustra should be included in one family (probably also some Escharæ & Milleporæ[47]).—
> That one Sertularia ~~would~~ is also included.—
> That the structure of the Flustraceæ is most widely different from the Clytias[48]. not only in the Polypus, but in the generation in the former case each ovule & Polypus has some intimate connexion. in the latter it is a young Polypus altered.— (Manner of growth?)
> General Anatomical discussion.—
> [added later in pencil] (Study Hydra & Actinia & my Madrepore & Sigillina in Blainville) (Sigillina & Polypus) [pencil note ends]
> That the connexion of the cells although not apparent in the true Flustræ must exist:

from similarity in growth & chain of gradation in the Capsule Flustræ: & in the Flustra of **P 234** & true Flustræ & Cellariæ having same body.—
That the Polypier is the essential part in the Corallines, it produces the cells & ~~young~~ in young Polypi (& after death of Polypus consequent on generation reproduces them?)—
That the mere possession of arms has grouped very heterogenious animals.—
That Corallina is a plant.—
[in pencil] Does it not emit in Suns rays gaz[49].— [pencil note ends] [continued on verso]
In Virgularia[50] does the truncate extremity correspond to ~~extremity of branch~~ root in Corallium[51] ? Examine extremities & the bag to extremity of branch.
The relative position of Polypier, with living mass in the Lamelliform.—
The structure of transparent extremities of Corallina.— Regrowth of Corallines when separated.
In the capsule Flustræ, cells without Polypi have capsules (Moveable)? Yes? I believe strong proof of disconnection.—
[p. 99 commences]
A close connection & co-sensation between the Polypi of many Corallines is established by the co-movements of "Capsules Flustras" of the setæ in Crisia[52]: the flashes of light in Clytia[53]: strongly seen in Virgularia, & in Alcyonium an injury in the stem causing all to collapse: whilst one *[illeg.]* being injured did not affect the mass.— on the other hand, one point in a Synoicum Blainv: affected all round it for some distance[54].—
Have not the Escaræ in the growth of the Polypier an analogy with the Celleporariæ: where cells appear formed in a cellular tissue (or group of hoods, or angular tubes as in Favosites) of a stone?—
A cell reproduces its Polypus
The stony striæ, on outside of Lobularia[55], connecting link with stony Zoophites.—
The Lobated ~~form~~ *[illeg.]* position of tentacula in Chiloe Actinia perhaps is an analogy in change between a Caryophyllia & Gorgonia or Corallium?— it shows a passage of this arrangement, without material change in animal.—
It is important to see in Clytia[48], substance included in a young cell appearing equally ready to form Polypus or Ovules.— the Coralline must produce this matter; not the Polypus the gemmule.—
I am inclined to think in Corallines, such as Tubularia[56] & Flustra, the Polypier is as much a living ~~man~~ being as any Plant, (as a Lichen or Corallina) that it communicates with the circumambient fluid either simply as in Clytia, or in more complicated manner, as in Flustra.
[continued on verso]
How little organization can be seen in Corallina, yet even the basic articulations produce paps with gemmules.— In the Polypier of the Flustraceæ it seems to make little difference, whether a central living axis is clearly visible or whether it (probably) forms a thin fold at the base of cells, in the encrusting Flustræ.—
I imagine in the Lamelliform Coralls, the Polypier is only an ~~ex~~ internal secretions, (a bony axis to give support) the Polypier being then the mass of living Matter: we see it thus in Virgularia[50].—

> There is an analogy between the corall-forming Polypi & turf-forming plants.— Hence here the soft matter ought to form the gemmules, as in the hard matter in the other cases.—
> I think there is much analogy between Zoophites & Plants, the Polypi being buds: the gemmules the inflorescence which forms a bud & young plant.—
> in Sertularia, the Capsules with gemmules appear to have no relation with any one Polypus; how could it form a totally different sort of capsule to its own, & in a place where it, the Polypus is never found.—
> [p. 99 ends]

It has been suggested by Sloan[45] that CD's intellectual development as a biologist was strongly influenced by his early contacts with Robert Grant[26] in Edinburgh, which steered him to pursue on the *Beagle* a programme of research on marine invertebrates oriented from the start in the direction of transmutation. However, the validity of this proposition has to be questioned. In the first place, CD paid no special attention to corallines during the first eight months of the voyage, and when he found his first specimen of *Flustra* what at once excited him was not the issue of whether it was a plant or an animal, but the remarkable properties of its vulture's beak capsules, the possibility that these organs might have any role in generation being scornfully dismissed. Later on, he worked out correctly many of the details of the anatomy of bryozoans that subsequently served to differentiate between their several families, and when he came across one belonging to what is now recognised as the phylum Entoprocta, he immediately spotted the essential diagnostic feature. Hence his studies on bryozoans were primarily an exercise in comparative anatomy, very similar in nature, and in the end less useful to him[15], than the observations on the numerous crustaceans that he dissected. Although some mention is made of changes taking place between related animals in his final two pages of notes, and analogies are suggested between hydrocorals and turf-forming plants, it is difficult to read into them views on the transmutation of species that he had not yet begun to develop seriously in any other context.

Very soon after returning to England in 1836, CD was disconcerted to find[57] that 'the Zoologists seem to think a number of undescribed creatures rather a nuisance', and was unable to obtain expert assistance with the classification of his marine invertebrates. Although Robert Grant[26], who was by then Professor of Zoology at University College London, did express an interest in some of the corallines, it was not followed up. CD wrote of Grant later[58] that 'He did nothing more in science — a fact which has always been inexplicable to me'. CD's original intention to give an account of some invertebrates in *The Zoology of the voyage of H.M.S. Beagle* therefore fell by the wayside, although from the introduction to *Journal of Researches* **2** it would appear that as late as 1845 it had not been finally abandoned. At this time, CD was still referring to the bryozoans as zoophytes, and there is no record of his ever knowing of the successful naming of the group in 1830 by Thompson[35] as Polyzoa. When in March 1837 he was writing on page 130 of the Red Notebook[59] that 'if one species does change into another it must be per saltum — or species may perish', Zoophytes and Polypi must already have begun to fade from the picture as far as he was concerned. There are indeed fewer than a dozen brief references to them in the whole series of Transmutation Notebooks[60].

There were of course many other terrestrial invertebrates such as insects and spiders to

which CD needed no introduction from Robert Grant, and which he collected avidly in a conventional way. He also took a great interest in the habits of some of the marine and terrestrial planarians that he found, which were free-living turbellarian flatworms now placed in orders Tricladida and Polycladida. In his paper published in 1844[61], a number of new species were described, though in the absence of further specimens from the areas of South America where he was working, they cannot always be assigned with certainty to a modern genus.

CD had less scope at the time of the voyage to theorise widely in discussing the animals that he collected than in his geological studies, but his *Zoology Notes* were nevertheless very much more than descriptions of the colouration and other details of his specimens that might be necessary for their taxonomic classification. At St Jago on 28 January 1832 he found an octopus among the rocks at low water, and recorded a splendid description of its changes in colour when he tried to grab hold of it, and of its responses on board the ship to the application of electric shocks and of being scratched. Seen under a lens he noted that the passing clouds of colour 'consisted of minute points apparently injected with a coloured fluid' — one of the earliest reports of the properties of their chromatophores. He was always interested in the locomotion of animals, and in the precise way in which they walked or ran or flew or swam, and soon we find him in Bahia (see p. 26) working out how the puffer fish *Diodon* takes up water by swallowing air in order to distend itself for regulation of its overall density and centre of gravity, and uses its pectoral fins after collapsing the caudals to enable itself, contrary to Cuvier's opinion, to swim while upside down. On the same day he caught a luminous click beetle, and critically examined the mechanism by which it bent its spine as a spring in order to jump suddenly into the air, this time finding grounds for disagreement with the account given in the *Dic. Class.* Next it was a migration of driver ants that attracted his attention, then the movements of some pulmonates, and a few weeks later (see p. 48) he came across 'the only butterfly I ever saw make use of its legs in running, this one will avoid being caught by shuffling to one side'. Many further examples could be quoted, among which one of the highlights would be his classical description (see p. 104) of the coating of the *Beagle*'s rigging off Monte Video by the gossamer web of spiders of family Linyphiidae that disperse by air. Others would be his accounts of the flights and feeding habits of *Rhynchops* (p. 159), humming birds (p. 235-6), condors (p. 254) and frigate birds (p. 300).

A field of biology of which CD was one of the founding fathers, together with Linnaeus, Buffon and Humboldt, was ecology, and many instances of his pioneering observations on the relations of animals with their environment are to be found in the *Zoology Notes*. Thus in May 1832 he wrote in Rio (see pp. 58-9):

> 'I could not help noticing how exactly the animals & plants in each region are adapted to each other.— Every one must have noticed how Lettuces & Cabbages suffer from the attacks of Caterpillars & Snails.— But when transplanted here in a foreign clime, the leaves remain as entire as if they contained poison.— Nature, when she formed these animals & these plants, knew they must reside together.—'

After the *Beagle*'s first visit to Tierra del Fuego in the southern summer of 1832-3, CD prefaced with an excellent account of the severity of the weather, backed up by some temperature records, some general observations correlating the climate with the growth of

trees, the formation of peat, and the populations of particular species of mammals, birds and insects. He noted on p. 134 that although the thermometer often rose to about 60° [Fahrenheit]:

> 'Yet there were no Orthoptera, few diptera, still fewer butterflies & no bees, this together with [the] absence of flower feeding beetles throughily [*sic*] convinced me how poor a climate that of Tierra del F. is'.

Visiting the Falkland Islands for the second time in April 1834, he wrote in a memorable passage on p. 215 about the marine zoology:

> 'Its main striking feature is the immense quantity & number of kinds of organic beings which are intimately connected with the Kelp. . . I can only compare these great forests to terrestrial ones in the most teeming part of the Tropics; yet if the latter in any country were to be destroyed I do not believe nearly the same number of animals would perish in them as would happen in the case of Kelp: All the fishing quadrupeds & birds (& man) haunt the beds, attracted by the infinite number of small fish which live amongst the leaves: . . . On shaking the great entangled roots it is curious to see the heap of fish, shells, crabs, sea-eggs, Cuttle fish, star fish, Planariæ, Nereidæ, which fall out. . . One single plant form is an immense & most interesting menagerie.— If this Fucus was to cease living, with it would go many: the Seals, the Cormorants & certainly the small fish & then sooner or later the Fuegian man must follow.— the greater number of the invertebrates would likewise perish, but how many it is hard to conjecture.'

He commented frequently, and often tested his observations experimentally, on the adaptation of marine animals to fresh water and *vice versa*, as when near Rio having found a fresh water snail in a lake often made salty by the sea, he asked: 'Is not this fact curious, that fresh water shells should survive an inundation of salt water? In the neighbouring Lagoon, Balani were adhering to the rocks.' Sometimes his speculations were perhaps a little wide of the mark, as on finding fresh water beetles in a stream at the Cape Verde islands 'supposed to be part of Atlantis' (see p. 371 of Specimen List); or when (see pp. 109 and 137) he found barnacles in the Rio Plata and at the Falkland Islands that he thought might be especially adapted for brackish and even for fresh water, possibly by keeping their opercula more 'throughily' closed in fresh water. But when he found beetles alive and swimming actively in the sea seventeen miles off Cape Corrientes[62] he decided that they had survived being washed down from the Rio Plata, and that this was 'a very instrumental means in peopling Islands with insects'.

In the *Zoology Notes* themselves there is no direct evidence as to when CD's belief in the stability of species began to be shaken, for he was still thinking about 'centres of creation' when he arrived in the Galapagos in September 1835[63], and still speaking of a Creator when he was musing about the lion-ant in Australia four months later[64,65]. His doubts about the immutability of species were first expressed when he was reorganising his notes some time between mid-June and August 1836, and writing about the Galapagos mocking birds *Mimus thenca* in his *Ornithological Notes*[64,66], said:

'These birds are closely allied in appearance to the Thenca of Chile or Callandra of La Plata. In their habits I cannot point out a single difference. They are lively, inquisitive, active, run fast, frequent houses to pick the meat of the Tortoise which is hung up, sing tolerably well; are said to build a simple open nest; are very tame, a character in common with the other birds. I imagined however its note or cry was rather different from the Thenca of Chile? Are very abundant over the whole Island; are chiefly tempted up into the high & damp parts by the houses & cleared land. I have specimens from four of the larger Islands: the two above enumerated [males from Charles and Chatham Islands]; a female from Albemarle Isd. and a male from James Island. The specimens from Chatham & Albemarle Isd appear to be the same; but the other two are different. In each Isld each kind is exclusively found: habits of all are indistinguishable. When I recollect the fact that [from] the form of the body, shape of scales & general size, the Spaniards can at once pronounce from which Island any Tortoise may have been brought. When I see these Islands in sight of each other, & possessed of but a scanty stock of animals, tenanted by these birds but slightly differing in structure & filling the same place in Nature, I must suspect they are only varieties. The only fact of a similar kind of which I am aware is the constant asserted difference between the wolf-like Fox of East & West Falkland Islds. If there is the slightest foundation for these remarks the zoology of Archipelagoes will be well worth examining; for such facts would undermine the stability of Species.'

Nevertheless, several of the issues to which he often returned earlier may give some indication as to how, albeit subconsciously, his ideas about evolution were taking shape. Thus he always asked himself whether the rats and mice, and other domestic animals, were indigenous or introduced species, and how much variation they displayed. Finding a rat on Goriti Island near Maldonado, he thought (see p. 171) because of its huge size and habits that it was 'an aboriginal', but the final decision[67] was that it was an extra large variety of the European *Mus decumanus*. A similar problem arose in relation to the black rabbits and other animals found in the Falkland Islands (see p. 209), but the rabbits had been released by early settlers[68] and resembled 'the cattle & horses, which are of as varying color as a herd in England'. CD once more thought that the mice were indigenous, but his specimens were eventually identified[69] as a variety of the European *Mus musculus*. It was clear on the other hand that no foxes had been introduced, and like three mainland species *Canis magellicanus*, *C. fulvipes* and *C. azarae* that he collected in Chile and Argentina, the two varieties of the Falkland fox *C. antarcticus*[70] proved to be indigenous. They were, however, all too approachable, and CD concluded: 'very soon these confident animals must all be killed: How little evidence will then remain of what appears to me to be a centre of creation.' In Ynche Island in the Chonos Archipelago (see p. 281) he found 'very many wild goats' whose 'color was pretty uniform' and which were evidently 'retrograding into their original figure & kind'.

Again, he was always assiduous in collecting the parasites of his specimens of all kinds, and having collected the lice from the native guinea-pig known as Aperea in Maldonado, commented (see p. 340):

> 'it would be interesting to compare these parasites with those inhabiting an Europæan individual to observe whether they have been altered by transportation: It would be curious to make analogous observation with respect to various tribes of men.'

Later he collected a louse in Chiloe (see p. 283) that he considered to be identical with those carried by the Patagonians at Gregory Bay, and quoted evidence from a surgeon from an English whaler for the existence of differences with those of Europeans; but this has not been confirmed[71]. Two of the first specimens that he collected in the Galapagos (see p. 412) were Acari from a marine iguana and from the Pudenda of a tortoise. He did not confine himself to vertebrate parasites, but also (see p. 87) noted their presence in the body cavity of a ctenophore.

He also took a particular interest in coprophagous beetles. Noting in Maldonado (see p. 175) 'the ample repast afforded by the immense herds of horses & cattle almost untouched', he continued:

> 'This absence of Coprophagous beetles appears to me to be a very beautiful fact; as showing a connection in the creating between animals as widely apart as Mammalia & Insects. Coleoptera, which when one of them is removed out of its original Zone, can scarcely be produced by a length of time & the most favourable circumstances.— The same subject of investigation will recur in Australia: If proofs were wanting to show the Horse & Ox to be aboriginals of great Britain I think the very presence of so many species of insects feeding on their dung, would be a very strong one.'

And commenting much later on specimen 3819 (not in spirits) he said:

> 'Very common beetle beneath dung on higher parts of St Helena. This is the most extraordinary instance yet met with of transportal or change in habits of stercovorous insects.'

In Australia the native beetles turned out to be largely restricted to wooded rather than pastoral areas, so that as in Maldonado the dung of cattle and horses remained uneaten. However, the several species of Scarabaeidae that CD found in Tasmania under the dung of cows (see p. 234) were probably native to the island, and had no difficulty in adjusting themselves to a new and copious supply of food. Not until the 1960s were programmes set up by CSIRO for the introduction of dung beetles from Africa and Europe to Australia in order to control dung-breeding pests of cattle and man, and at the same time to bury more dung with consequent improvement of the pasture[72]. The dung beetles in St Helena were presumably of African origin, and able to make do with mouse dung.

A further theme with obvious implications for the species problem was the geographical distribution of different species, and their isolation on islands or by mountain ranges. Arriving at the Falkland Islands for the first time on 1 March 1833, just after the British flag had first been hoisted, he found it 'one of the quietest places we have ever been to', and with all the boats away had little to occupy him except for his thoughts. These he noted down in his pocketbook, and they include the following queries and comments[73]:

'March 2. Falkland—
To what animals did the dung beetles in S. America belong — Is not the closer connection of insects and plants as well as this fact point out closer connection than Migration.
Scarcity of Aphidians?
The peat not forming at present & but little of the Bog Plants of Tierra del F; no moss; perhaps decaying vegetables may slowly increase it. — beds ranging from 10 to one foot thick.
Great scarcity in Tierra del of Corallines, supplanted by Fuci: Clytra prevailing genus.
Tuesday 12th —
Examine Balanus in fresh water beneath high water mark.
Horses fond of catching cattle — aberration of instinct.
Examine pits for Peat. Specimen of do — Have there been any bones ever found &c or Timber.
Are there any reptiles? or Limestone?
21st
Saw a cormorant catch a fish & let it go 8 times successively like a cat does a mouse or otter a fish; & extreme wildness of shags.
22nd.
East of basin, peat above 12 feet thick resting on clay, & now eaten by the sea. Lower parts very compact, but not so good to burn as higher up; small bones are found in it like Rats — argument for original inhabitants: from big bones must be forming at present, but very slowly: Fossils in Slate: opposite points of dip: & mistake of stratification: What has become of lime?
It will be interesting to observe differences of species & proportionate Numbers: what also appear characters of different habitations.
Migration of geese in Falkland Islands as connected with Rio Negro?'

There are not many direct references in the *Zoology Notes* themselves to the geographical distribution of different species of mammals and birds except (see pp. 188-90) in the case of the ostrich that CD called the 'Avestruz Petise'. This was named *Rhea Darwinii* by Gould, when he mounted the specimen shot by Conrad Martens at Port Desire in January 1834[74], which was partly eaten before CD had realised that it belonged to a smaller and darker species than the *R. Americana*, that was common further to the north. The two birds came to provide the best known example of the manner in which closely related species with overlapping ranges replaced one another in proceeding southwards over the continent. There was next an essay written on board the *Beagle* in 1834 by CD[75] entitled 'Reflection on reading my Geological Notes', in which he developed a narrative framework for the history of life on the continent, and listed the mammals that could reasonably have migrated sequentially southwards from their northern original homes. And in two relevant notes on some of the birds of Chile[76] he wrote:

'These forms appear to our eyes singular to be the common birds throughout an extensive country. In T. del Fuego the Certhia & Troglodytes were the two most abundant kinds. In central Chile both are found, but extremely few in numbers. In that

> country (& in a like manner in a like case in other countries) one is apt to feel surprise that a species should have been created, which appears doomed to play so very insignificant a part in the great scheme of nature. One forgets that these same beings may be the most common in some other region, or might have been so in some anterior period, when circumstances were different. Remove the Southern extremity of America, & who would have supposed that Certhia, Troglodytes, Myothera, Furnarius had been the common birds over a great country.'

and

> 'It appears to me, that when the lists & collections of birds made in the different parts of S. Southern America are compared, a large number will be found to have surprisingly large geographic ranges. No doubt the similarity in physical constitution of the country; over T. del Fuego & the whole west coast as far north as Concepcion; & again between Patagonia, the lofty valleys of the Cordillera, & northern Chili; & lastly but in a much lesser degree between La Plata & central Chili, is the chief cause of this fact. I should observe, that in the few cases where I have spoken of Lima (Lat 12°) as the Northern Habitat of any species; it is probable that the real boundary lies ten degrees further north (near C. Blanco), where the arid open country of Peru is converted into the magnificent forest land of Guyaquil.'

It is probable, however, that these passages were added to the *Ornithological Notes* shortly after the return of the *Beagle* to England. For in a document now filed with his unpublished *Beagle* Animal (*i.e.* mammal) Notes[77], he drew up long lists of the closely related birds and mammals found on the east and west sides of the Andes, and considered possible reasons for their distribution. The *Animal Notes* were headed 'Gt Malbro' [St], where starting on 13 March 1837 he lived for 21 months in furnished rooms with his secretary and servant Syms Covington, so that such material belongs strictly to the period after the end of the voyage when he had already begun to develop his ideas on the transmutation of species. Nevertheless, the role of geographical distribution was clearly in his thoughts very early on.

The second field of biology to whose establishment CD made major contributions was the study of animal behaviour[78,79]. Most significantly, he appreciated from the start that behaviour was an important factor to be taken into account in identifying a species, as in the case mentioned on p. 50 of the butterflies which shuffled to one side, '& which from appearance & habits were I am sure the same species'. The following year (see p. 211) he noted that the carrion-feeding hawk caracara had a 'connection in habit as well as in structure with true Hawks'. Other examples could be quoted, and it was possibly the close similarity in habits of the various Geospizinae in the Galapagos except for the cactus finch (see p. 297), that deterred him from appreciating their significance when he saw them, though at the same time it was behavioural differences between the mainland species of mocking bird that had led him to distinguish *Mimus orpheus* in Monte Video from *M. patagonicus* on the Rio Santa Cruz.

There are many vivid descriptions of the behaviour of animals at all levels, from the ants in Bahia (see p. 29), through spiders spinning their webs and wasps preying on them (see p. 38), the 'monstrous' coconut crabs in the Cocos Keeling Islands (see p. 311), penguins and

steamer-ducks in the Falklands (see p. 213), to the herds of guanaco on the pampas (see p. 181-2). CD's speculations on the underlying reasons, such as the attribution to an instinct 'to find new countries' that leads flocks of butterflies to fly out to sea (see p. 121), are not always successful. The motivation of the biscatche for collecting large piles of rubbish in front of their holes (see pp. 180-1) is described in more anthropomorphic terms than would be acceptable today, but this does not detract from the liveliness of his accounts, nor from his purposeful correlation of behaviour with details of structure and environment.

In this field, as in all else, CD was a superbly skilful and accurate observer who thanks to his intensely analytical approach invariably made a highly effective use of the opportunities offered to him, whether to conduct studies of the comparative anatomy of marine invertebrates, or to examine the distribution, ecology and behaviour of a wide range of terrestrial animals. He was thus enabled to examine the animals occupying many different environments, and had the very good fortune to be taken by the *Beagle* to the Galapagos, which turned out eventually to be an ideal place, rivalled only by Hawaii and Madagascar, for studying the evolution of new species in isolated islands. In addition, the *Beagle* landed him at places where exceptionally informative fossils were lodged in the cliffs, and enabled him to visit the Andes and the coastal plains on either side of the continent where there was much for a geologist to learn about the formation of a mountain range and the accompanying rise and fall of the land. It might not be an exaggeration to say that he was exposed in those five years to more new facts than any previous scientist, and such were his talent for observation and his genius afterwards to arrive by hard thinking at fundamentally new explanations for what he had seen, that *On the Origin of Species* was the inevitable outcome.

CD himself summed up the whole story rather nicely in a letter to his sister Catherine written from Maldonado on 22 May 1833[80]:

> 'I am quite delighted to find the hide of the Megatherium has given you all some little interest in my employments. These fragments are not however by any means the most valuable of the Geological relics. I trust & believe that the time spent in this voyage, if thrown away for all other respects, will produce its full worth in Nat: History. And it appears to me the doing what little one can to encrease the general stock of knowledge is as respectable an object of life as one can in any likelihood pursue. It is more the result of such reflections (as I have already said) than much immediate pleasure which now makes me continue the voyage. Together with the glorious prospect of the future, when passing the Straits of Magellan, we have in truth the world before us. Think of the Andes; the luxuriant forest of the Guayquil; the islands of the South Sea & new South Wale[s]. How many magnificent & characteristic views, how many & curious tribes of men we shall see. What fine opportunities for geology & for studying the infinite host of living beings: is not this a prospect to keep up the most flagging spirit? If I was to throw it away, I don't think I should ever rest quiet in my grave: I certainly should be a ghost & haunt the Brit. Museum.'

So now let his *Zoology Notes* speak for themselves.

Endnotes to Introduction

1 *Beagle Diary* p. 4.
2 In June 1833 the Captain gave him all the drawers in the poop cabin formerly belonging to John Lort Stokes, mate and surveyor, so that he had it to himself (see *Correspondence* **1**:313); and to accommodate his specimens, he had in addition a very small cabin under the forecastle. See Vol. 1, pp. 218-24 of *The life and letters of Charles Darwin*. Edited by Francis Darwin. John Murray, 1887.
3 *Narrative* **1**:385.
4 R. Fitz-Roy (1836) Sketch of the Surveying Voyages of his Majesty's Ships Adventure and Beagle, 1825-1836. *J. Royal Geog. Soc. Lond.* **6**:311-43.
5 Cambridge University Library MSS: DAR 32-3 *Diary of observations on the geology of the places visited during the voyage*. Parts I and II; DAR 34-8 *Notes on the geology of the places visited during the voyage: maps, etc.* Parts I-V.
6 Nora Barlow, ed. *Darwin and Henslow. The growth of an idea. Letters 1831-1860.* John Murray, 1967; and *Correspondence* **1**.
7 Charles Darwin (read 7 March 1838) On the connexion of certain volcanic phenomena in South America; and on the formation of mountain chains and volcanos, as the effect of the same power by which continents are elevated. *Transactions of the Geological Society of London*, 2nd ser. pt. 3, 5 (1840):601-31. Reprinted in *Collected Papers* **1**:53-86.
8 *Narrative* **3**.
9 *Journal of Researches* **1**.
10 *Journal of Researches* **2**.
11 *The structure and distribution of coral reefs* etc. Also *Geological observations on the volcanic islands visited during the voyage of H.M.S. Beagle* etc. And *Geological observations on South America* etc. London, Smith Elder and Co.
12 *Autobiography* p. 116.
13 *Correspondence* **1**:379-82.
14 *Correspondence* **1**:315-17.
15 *Autobiography* pp. 77-8.
16 Sandra Herbert (1991) Charles Darwin as a prospective geological author. *British Journal of the History of Science* **24**:159-92. And see also Sandra Herbert (1977) The place of man in the development of Darwin's Theory of Transmutation. Part II. *Journal of the History of Biology* **10**:155-227.
17 *Beagle Diary* pp. 22-7.
18 *Autobiography* p. 159.
19 *Correspondence* **6**:514.
20 *Autobiography* p. 119.
21 *Beagle Diary* p. 21, and letter from John Coldstream of 13 September 1831 in *Correspondence* **1**:151-3.
22 In the *Zoology Notes* the supply of paper with a red marginal line seems to have been exhausted at **CD P. 315**.
23 *Autobiography* pp. 77-8.
24 *Proceedings of the Royal Society of London* **44**:i-xxv (1888).
25 This instrument, manufactured by Bancks & Son of 119 New Bond Street, had been

recommended to him by Robert Brown. See letters to Susan Darwin of 6 September 1831, and to W.D. Fox of 23 May 1833, in *Correspondence* **1**:143-5 and 315-17.

26 Robert Edmond Grant (1793-1874) was a local physician and lecturer in comparative anatomy at Edinburgh University when CD was a student there in 1825-1827, and was Professor of Zoology and Comparative Anatomy at University College London 1827-1874. CD accompanied him on local expeditions around Edinburgh, and was closely associated with his researches on marine invertebrates.

27 Cambridge University Library MS DAR 118.

28 For a list of the books on board the *Beagle* see *Correspondence* **1**:553-66.

29 Q. Bone, H. Kapp and A.C. Pierrot-Bults (1991) *The Biology of Chaetognaths*. Oxford University Press. See also C. Nielsen (1995) *Animal Evolution. Inter-relationships of the Living Phyla.* Oxford University Press.

30 Charles Darwin (1844) Observations on the Structure and Propagation of the Genus *Sagitta*. *Annals and Magazine of Natural History, including Zoology, Botany, and Geology* **13**:1-6. Reprinted in *Collected Papers* **1**:177-82.

31 *A monograph on the sub-class Cirripedia, with figures of all the species. Vol. I. The Lepadidae, or pedunculated Cirripedes. Vol. II. The Balanidae, or sessile Cirripedes; the Verrucidae, etc., etc., etc.* The Ray Society, London, 1851 and 1854.

32 John V. Thompson (1830) Memoir IV. On the Cirripedes or Barnacles; demonstrating their deceptive character; the extraordinary Metamorphosis they undergo, and the Class of Animals to which they indisputably belong. *Zoological Researches and Illustrations* . . . King and Ridings, Cork.

33 John Ellis (1755) *An essay towards a natural history of the corallines, and other marine productions of the like kind, commonly found on the coasts of Great Britain and Ireland. To which is added the description of a large marine polype.* London, 1755.

34 R.E. Grant (1827) Observations on the Structure and Nature of Flustræ. *Edinburgh New Philosophical Journal* **3**:107-18; 337-42. The paper was read before the Wernerian Natural History Society on 24 March 1827, three days before CD presented the contribution of his own to the Plinian Society that is reproduced in *Collected Papers* **2**:285-91.

35 John V. Thompson (1830) Memoir V. On Polyzoa, a new animal discovered as an inhabitant of some Zoophites — with a description of the newly instituted Genera of Pedicellaria and Vesicularia, and their Species. *Zoological Researches and Illustrations* . . . King and Ridings, Cork.

36 John Ryland (1970) *Bryozoans*. Hutchinson, London.

37 Edward Griffith and others. *The animal kingdom arranged in conformity with its organization by the Baron Cuvier . . . with supplementary additions to each order.* 16 vols. Edinburgh, 1827-35. See also *Cuvier*, 2nd edition, vols. 4, 5.

38 S.F. Harmer (1862-1950), later Sir Sidney Harmer FRS, was in 1901 Superintendent of the University Museum of Zoology in Cambridge, when with the aid of CD's Specimen lists lent to him by Francis Darwin he identified a number of the specimens of marine invertebrates presented some years earlier to the Museum.

39 *Journal of Researches* **1**:258-62 and **2**:201-3.

40 Judith Winston (1984) Why bryozoans have avicularia — a review of the evidence. *Novitates No. 2789.* American Museum of Natural History, New York.

41 *Lamouroux* p. 66.

42 Letter from CD to Henslow of 24 July to 7 November 1834 in *Correspondence* **1**:397-403.
43 *Plant Notes* pp. 194-5.
44 Letter from CD to Catherine of 20-29 July 1834 in Correspondence **1**:391-4.
45 Phillip R. Sloan (1985) Darwin's invertebrate program, 1826-1836: Preconditions for transformism. Chapter 3, pp. 71-120 in *The Darwinian Heritage*, edited by David Kohn. Princeton University Press.
46 This has turned out not to be entirely true, since calcification of the zooids is characteristic of the Cheilostomata as opposed to the Ctenostomata.
47 The first four of these are indeed bryozoans, but Milleporae are hydrocorals.
48 *Clytia*, formerly included with bryozoans among the Sertularians, is a hydrozoan of order Leptothecata.
49 In a Memoir sent by CD to W.H. Harvey at the Herbarium of Trinity College Dublin on 7 April 1847 (*Correspondence* **4**:29) he said of observations made at Bahia on either the coralline alga *Melobesia* or on *Halimeda* in August 1836 that 'on several occasions having kept vigorous tufts of articulated Nulliporæ in sea-water in sun-light, it appeared as if a good deal of gas was exhaled; it w^{d} be curious to ascertain what this is.' That bubbles of oxygen were released under such conditions had first been observed by Joseph Priestley in 1777, and was described more fully in 1779 by Jan Ingen-Housz in his book on *Experiments on Vegetables*.
50 *Virgularia* is a sea pen, a hydrozoan octocoral of order Pennatulacea.
51 *Corallium* is a brightly coloured octocoral of order Gorgonacea, but no specimen is recorded in the *Zoology Notes* or *Specimen Lists*.
52 CD's *Crisia* was not in fact this genus, but the anascan bryozoan *Caberea minima*, the coordinated movements of whose vibracula he described very nicely.
53 Bioluminescence is indeed common in cnidarians, and its propagation is controlled by their primitive nervous systems.
54 CD has here concluded perceptively that the coordinated movements of the vibracula in a bryozoan, the flashes of light in the thecate hydroid *Clytia* and the coral *Virgularia*, and the spread of injury in another coral and the tunicate *Synoicum*, indicate that all these 'heterogenious' animals must somehow be capable of internal communication between their individual polyps, and therefore heralds the first appearance of nervous systems in the eumetazoa. (See, for example, Chapter 9 by J.P. Thorpe on *Bryozoa* in *Electrical conduction and behaviour in "simple" invertebrates*, edited by G.A.B. Shelton. Clarendon Press, Oxford, 1982.) This crucial stage in the evolution of higher animals was reached in the cnidarians some 550 Ma ago (see Bertil Hille (1992) Evolution and diversity. Chapter 20 in *Ionic channels of excitable membranes*. 2nd edition. Sinauer Associates, Sunderland, Massachusetts.) It has also been pointed out recently by Richard Keynes & Fredrik Elinder (1999) *The screw-helical voltage gating of ion channels. Proc. R. Soc. Lond.* B **266**:843-52 that across the whole of the animal kingdom, voltage-gated ion channels of every type have genes in which several critical features have been perfectly conserved since that same era, though CD's addition of bryozoans to the list of animals that possess primitive nervous systems remains to be followed up by a detailed examination of the innervation of avicularia and vibracula, and by the cDNA sequencing of the ion channels in their nerve fibres.
55 *Lobularia* is a soft coral of order Alcyonacea, dead men's fingers, in which the

coenenchyme is sclerite-filled.
56 *Tubularia* is not a bryozoan, but a hydroid of suborder Anthoathecata.
57 Letter from CD to Caroline Darwin of 24 October 1836 in *Correspondence* **1**:509-10.
58 *Autobiography* p. 49.
59 Sandra Herbert (ed.) (1980) *The Red Notebook of Charles Darwin*. British Museum (Natural History) and Cornell University Press.
60 Paul H. Barrett, Peter J. Gautrey, Sandra Herbert, David Kohn and Sydney Smith (eds.) (1987) *Charles Darwin's Notebooks, 1836-1844*. British Museum (Natural History) and Cambridge University Press.
61 Charles Darwin (1844) Brief descriptions of several terrestrial *Planariae*, and of some remarkable marine species, with an account of their habits. *Annals and Magazine of Natural History, including Zoology, Botany and Geology* **14**:241-51. Reprinted in *Collected Papers* **1**:182-93.
62 See entry for Specimen 875 (not in spirits); and *Journal of Researches* **2**:158-9; also *Insect Notes* pp. 66-7.
63 *Beagle Diary* p. 356.
64 R.D. Keynes (1997) Steps on the path to the Origin of Species. *Journal of Theoretical Biology*. **187**:461-71.
65 *Beagle Diary* pp. 402-3.
66 *Ornithological Notes* p. 262.
67 *Zoology* **2**:31-4.
68 *Zoology* **2**:92.
69 *Zoology* **2**:38.
70 *Zoology* **2**:7-16.
71 *Insect Notes* pp. 43-4 and 88.
72 Information provided by Lindsay Barton Browne, formerly leader of the CSIRO program on 'Biological control of dung and dung breeding flies'. Dung beetles from southern Africa were introduced in northern Australia with limited success to control the buffalo fly, a blood sucking pest of cattle, and with greater success European beetles were introduced in south-eastern Australia to control another dung-breeding nuisance pest of man and cattle, the bushfly.
73 *Beagle Diary* pp. 144-9; and *CD and the voyage* pp. 177-9.
74 *Beagle Diary* p. 212; *Ornithological Notes* pp. 268-76; and *Zoology* **3**:123-5.
75 Sandra Herbert (1995) From Charles Darwin's portfolio: an early essay on South American geology and species. *Earth Sciences History* **14**:23-36.
76 *Ornithological Notes* pp. 259-60.
77 Cambridge University Library MS DAR 29.1.
78 Richard Burkhardt (1985) Darwin on animal behaviour and evolution. *Darwinian Heritage* Chapter 13, pp. 327-65.
79 Patrick Armstrong *Darwin's Desolate Islands: a Naturalist in the Falklands, 1833 and 1834*. Picton Publishing (Chippenham) Ltd., 1992. Also: An ethologist aboard HMS *Beagle*: the young Darwin's observations on animal behaviour. *Journal of the History of the Behavioural Sciences* **29**:339-44, 1993.
80 Letter from CD to Catherine Darwin of 22 May-14 July 1833 in *Correspondence* **1**:311-15.

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Note on editorial policy

My aim has been to adopt the majority of the practices laid down and explained in full by the editors of *The Correspondence of Charles Darwin*, introducing a few changes only in the interests of making the text as easily readable as possible. One departure from convention has been to retain CD's underlining and double underlining as it stands in the manuscript, reserving italics to be used in the customary way in the footnotes for the Latin names of genera and species in former or current use. Liberties have been taken where necessary with CD's sometimes erratic punctuation, further complicated by the not infrequent dots, which have been omitted when they can reasonably be regarded as 'pen rests', but have otherwise been retained as commas or full stops according to the sense of the passage. CD's own idiosyncratic spelling of words such as *broard* and *throughily* is always preserved, but mistakes that are clearly a slip of the pen have been corrected, and missing letters have been inserted in square brackets. Where there is doubt, and there is no difficulty in deciding what his intention should have been, for example in the case of adding the final s to the plural of a noun, I have given him the benefit of it. Where it is hard to decide whether a word starts with a lower case or a capital letter, I have used a capital in the cases of proper names and places. His abbreviations appear as nearly as possible as they are written, with '&' almost invariably used in place of 'and'. Relatively few words have been crossed out by CD during the writing, and such corrections have been retained in the text rather than listing them separately, as has any later over-writing of a single letter. Round brackets used occasionally by CD are retained. Editorial interpolations are in square brackets. Italic square brackets enclose conjectured readings and descriptions of illegible passages. Material that is irrecoverable because the manuscript has been torn or damaged is indicated by angle brackets < >, and any text within them is the editor's. CD's paragraphing has in general been retained, with a fresh paragraph for each new entry, except that for entries running for more than a page, breaks have sometimes been introduced when the subject changes, in order to avoid overlong paragraphs.

A number of pages of the text have later been lined through vertically, not because CD wished to delete them, but to indicate that the material had been incorporated in a subsequent publication.

Many important footnotes, identified in the margin as (a), (b), (c) etc. placed opposite the passages to which they refer, were added later by CD, generally on the back of the page on which he had been writing. Those that were clearly almost immediate afterthoughts or corrections have been incorporated at the most appropriate point in the text itself. Those that were evidently written at a later, though not always recorded date, have been distinguished by their relegation to separate paragraphs.

The pages were numbered right and left at the top of each page, generally with the year in the margin beneath, and the month beside it, with the place in the centre of the page. The topic was always entered, underlined, in the margin at the head of each page. The year, month and place appear in the headings of each of the printed pages, as far as possible retaining CD's description of the place. CD's not infrequent cross referencing to his own pages is entered in heavy type as **'CD P. 00'**, as are editorial references to places in the manuscript where the text continues after the insertion of one of his notes, or a group of

editorial footnotes. The pagination of the manuscript is shown by the numbers in heavy type between vertical lines, thus |**000**|.

Principal sources of references

Journal of Researches **1**
1st edition: Narrative of the surveying voyages of His Majesty's Ships Adventure and Beagle, between the years 1826 and 1836, describing their examination of the southern shores of South America, and the Beagle's circumnavigation of the globe. Volume III. Journal and remarks. 1832-1836. By Charles Darwin Esq., M.A. Sec. Geol. Soc. Henry Colburn, London, 1839.

Journal of Researches **2**
2nd edition: Journal of Researches into the Natural History and Geology of the Countries visited during the Voyage of H.M.S. Beagle under the Command of Capt. Fitz Roy, R.N. By Charles Darwin, M.A., F.R.S. John Murray, London, 1845.

Zoology **1**
The zoology of the voyage of H.M.S. Beagle under the command of Captain FitzRoy, R.N., during the years 1832 to 1836. Edited and superintended by Charles Darwin, Esq. M.A. F.R.S. Sec. G.S. Naturalist to the expedition. Part I. Fossil mammalia: by Richard Owen, Esq. F.R.S. Smith, Elder and Co., London, 1840.

Zoology **2**
The zoology of the voyage of H.M.S. Beagle . . . Part II. Mammalia by George R. Waterhouse, Esq. Smith, Elder and Co., London, 1839.

Zoology **3**
The zoology of the voyage of H.M.S. Beagle . . . Part III. Birds, by John Gould, Esq. F.L.S. Smith, Elder and Co., London, 1841.

Zoology **4**
The zoology of the voyage of H.M.S. Beagle . . . Part IV. Fish, by The Rev. Leonard Jenyns, M.A., F.L.S. Smith, Elder and Co., London, 1842.

Zoology **5**
The zoology of the voyage of H.M.S. Beagle . . . Part V. Reptiles, by Thomas Bell, Esq., F.R.S., F.L.S. Smith, Elder and Co., London, 1843.

Cirripedia
A monograph of the sub-class Cirripedia, with figures of all the species. The Balanidæ, (or sessile cirripedes); the Verrucidæ, etc., etc., etc. By Charles Darwin, F.R.S., F.G.S. The Ray Society, London, 1854.

Planaria
Brief descriptions of several terrestrial *Planariae*, and of some remarkable marine species, with an account of their habits. By Charles Darwin. *Annals and Magazine of Natural*

History, including Zoology, Botany, and Geology **14**:241-51 (1844). Reprinted in *Collected papers* **1**:182-93.

Origin of Species
On the Origin of Species by means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. By Charles Darwin. John Murray, London, 1859.

Beagle Diary
Charles Darwin's *Beagle* Diary. Edited by Richard Darwin Keynes. Cambridge University Press, 1988.

Beagle Record
The *Beagle* Record. Selections from the original pictorial records and written accounts of the voyage of H.M.S. Beagle. Edited by Richard Darwin Keynes. Cambridge University Press, 1979.

Ornithological Notes
Darwin's Ornithological Notes. Edited by Nora Barlow. *Bulletin of the British Museum (Natural History)*. Historical Series. Vol. 2(7):201-78. 1963.

Insect Notes
Darwin's Insects. Edited by Kenneth G.V. Smith. *Bulletin of the British Museum (Natural History)*. Historical Series. Vol. 14(1):1-123. 1987.

Plant Notes
Darwin's notes on *Beagle* plants. Edited by Duncan M. Porter. *Bulletin of the British Museum (Natural History)*. Historical Series. Vol. 14(2):145-233. 1987.

Oxford Collections
Charles Darwin's *Beagle* collections in the Oxford University Museum. Edited by Gordon Chancellor, Angelo DiMauro, Ray Ingle and Gillian King. *Archives of Natural History* Vol. 15:197-231. 1988.

Autobiography
The Autobiography of Charles Darwin 1809-1882. Edited by Nora Barlow. Collins, London, 1958.

CD and the Voyage
Charles Darwin and the Voyage of the Beagle. Edited by Nora Barlow. Collins, London, 1945.

Collected papers **1** and **2**
The Collected Papers of Charles Darwin. Edited by Paul H. Barrett. 2 vols. University of Chicago Press, Chicago and London, 1977.