Concepts of Evolutionary Theory and Biogeography

——Through a Comparison of Darwin and Wallace——

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Abstracts

The existence of a global British ethos from the 18th century to the 19th century such as the development of the philosophy of the European Enlightenment, the Industrial Revolution and colonial expansion was established as the social background for the establishment of evolutionary biogeography. Darwin has denied creationism and catastrophic theory to develop uniformitarian theory and gradualism together with confirming global biodiversity. As a result, the surprising diversity of the species all over the world and the fact that species of living creature differ according to location even if the basic environment is the same became evident. This does not conform with creationism whereby species must have been created in perfect compatibility with the environment. Also catastrophic theory was considered to have been refuted by Lyell's uniformitarian theory.

Whilst creationism was being refuted 19th century, the elucidation of the process of dispersal and divergence from a common progenitor in one original place was required in order to establish the successive temporal and spatial evolution of living things. The direction of research into this kind of biogeography of the distribution of living things concurred with the biological paradigm shift that was the proposal of evolutionary theory.

With these circumstances as a background, Darwin conceived the theory of evolution from the consideration of the distribution of living things. Initially, Darwin thought that the individual variations of living things were caused by exposure to a new environment. "Geographical isolation" was taken to be important as a principal component of this speciation and research into the migration and diffusion of living things was conducted. However Darwin thought that if there is sufficient time, and physical and ecological barriers are removed then a species will spread throughout the world. Darwin initially considered the impact of a geographical barrier with regards to speciation however he came to stress the mechanism of fortuitous transport

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as the cause of this diffusion and geographical distribution. Furthermore through carrying out observations and research into particles after his return to Great Britain, Darwin understood the large quantity of variation in the natural world even in the same environment. In short, the variation of living things occurs even without geographical or geological change.

Meanwhile in contrast to Darwin, Wallace spent his life considering the relationship between evolution and geographical distribution in his theory, and continued to explain the influence changes in the geographical factors of the environment have on the distribution of living things and evolution. He stressed changes in the Earth's crust such as upheaval and subsidence as impacts had on the distribution and isolation of living things.

This is also reflected in the differences between Darwin's and Wallace's theories of evolution. In Darwin's *Origin of Species,* the main constituent of evolution is very much the bion. An individual in a species occupies various positions and locations in connecting with the ecosystem, the individual proactively adapts to those conditions and variation is produced. At length, the variation of each individual accumulates on average, the whole species diverges and new species are formed. In contrast, Wallace's evolutionary theory states that the unit of evolution is variation; only variations to adapt to changes in environmental conditions such as ensuring a food supply occur; and these evolve into a new independent species.

This is to say, Darwin's theory of evolution recognised the diversity of the random changes of many individuals.

Thereafter, Darwin's theory of evolution was introduced to Germany by Haeckel and started to spread. Biogeographical and ecological theory came to be introduced to geography by Ratzel who was strongly influenced by Haeckel.

However Haeckel's concept differed to that of Darwin in that it depended on orthogenesis. Also although the biology of Haeckel broke down the concept of natural theology in Germany, it was on the other hand, an organic monism that was strongly influenced by the ideology of romanticism. The geography of Ratzel, which received this kind of ideology from Haeckel, can be thought to be inclined towards a holistic theory of social organism.

I Introduction

Biology has often been seen as a_ problem in traditional research into geographical history and geographical methodology especially in its relationship with ecological methodology. The historical trend of geographical thought was to take Humboldt's physionomie and concepts of life form as an ecological start point and attempt to seek the effects in Ratzels *Anthoropogeographie* by means of Haeckel's Darwinism[1]. That is to say, the systems of methodology such as ecology and furthermore chorology as the morphology and functional theory from Haeckel

were thought to be received in geography as an effect of evolutionary theory. Also, ecological methodology from the German Ratzel was spreading to French, British and American geography[2].

Incidentally, was Darwin's theory of evolution likely to have been applied to the methodology of human geography without modification? Stoddart points out that geographers are almost entirely unfamiliar with the concept of "randomness in the initial stage of variation" that appears in Darwin's theory[3]. Furthermore, according to Livingstone, the worldview according to the natural theology of the first half of the 19th century in which divine providence and the uniformity of nature was stressed was liberated by Darwin's theory of evolution, and a movement towards new laws of nature began. However Livingstone claims it was not Darwin's own notions which had a direct impact on geography but rather the introduction of concepts of heredity of acquired character and orthogenesis from Neo-Lamarckism and the contribution made by the introduction of environmental determinism to geography[4].

Also, according to recent research on the history of biology, Bowler contends that the previously noted Haeckel cannot be considered a legitimate successor to Darwinism. That is to say, in the evolutionary theory of Darwin and Wallace, variation selected by the environment is essentially random and directionless. It is a small variation routinely utilised in the identification of individual animals and humans. The fact that variation has no directionality shows that the process of evolution directed by adaption alone is incidental and divergent in form. Evolution is a fortuitous branching divergent process of adaption, migration and dispersal. Lamarck, Haeckel and Huxley recognised an orthogenetic perspective with regards to this. These morphologists considered nature to be constructed from logical patterns and tried to comprehend the laws governing the structures of organisms derived from a purely morphological perspective. From a position which emphasised growth as analogous to development, evolution moves towards a target in a correct sequence and is the development of an exactly planned pattern. Consequently, morphologists Haeckel and Huxley cannot be said to be true successors or supporters of Darwinism. Darwin's theory was succeeded more accurately by Wallace et al., who

1) Ratzel, F., *Anthropogeogaphie,* Verlag von J. Engelhorns Nache, 1882.

2) Dickinson, R. E. *Regional ecology*—The study of mans environment, John Wiley & Sons, 1970.
Martin, G. J., *All possible worlds*—*A history of geographical ideas, fourth edition,* Oxford University Press, 2005.

3) Stoddart, D. R., 'Darwins impact on geography5, *Annals of Association of American Geographers,* 56, 1966, pp. 683-698.

4) Campbell, J. A. and Livingstone, D. N., 'Neo-Lamarckism and the development of geography in the United States and Great Britain, *Transactions of Institute of British Geographers New Ser.,* 8, 1983, pp. 267-294.
Livingstone, D. N., 'Natural theology and Neo-LamarcKism: the changing context of nineteenth-century geography in the United States and Great Britain, *Annals of Association of American Geographers,* 74, 1984, pp. 9-28.

stressed the geographic side of biological distribution rather than by the morphologists[5].

Therefore, the ingression and reception of Darwinism in geography was carried out through amendments by the intermediary Haeckel, suggesting the necessity of reappraising the influence Darwin and Wallace have since had on geography.

Accordingly I would like organise the above kinds of research trends in geographical history and to clarify the following issues in particular.

Firstly, I would like to clarify why Darwin and Wallace arrived at the conception of evolutionary theory from the issue of the distribution of organisms in the primitive morphology of modern geography, in which the boundaries of biology, natural history and geography are undifferentiated.

Secondly, in addition to methodological genealogy since Humboldt, which led to ecology from research into geobotany, the landscape of vegetation and morphology, what was the impact of the awareness of the issues of zoogeography, namely distributional region, isolation and geographical speciation? There is probably a need to reappraise geographical history directly based on the evolutionary theory of Darwin and Wallace in Great Britain prior to geography being influenced by Germany's Haeckel and Ratzel.

Thirdly, Wallace's evolutionary theory showed a greater concern for the geographical distribution of organisms in comparison to that of Darwin. I would like to clarify the biogeographical nature of the evolutionary theory of both Wallace and Darwin by comparison.

II Darwin's Biogeographical Considerations and the Conception of Evolutionary Theory

(1) Evolutionary Prehistory

As historical geographical methodologies relating to modern science, the geographical history researcher Livingstone raises several points of research into spatial significance, such as ①Research relating to spaces produced by science (scientific space/topos and research relating to the spatial networks of humans and objects involving science), ②Research concerning the contextualization of science and ③The spatial expression of scientific results (E. g. the development of cartography etc.)[6]

Here, let's get a perspective of the relationship between biogeography since Darwin and Wal-

5) Bowler, P. J *Evolution: the history of idea,* The University of California Press, 1984. Bowler, P.. J *The Non-Darwinian revolution: reinterpreting a historical myth.* Baltimore: The John Hopkins University Press, 1988.

6) Livingstone, D. N., 'The spaces of knowledge－contributions towards a historical geography of science,, *Environment and Planning Ser. D: Society and Space,* 13, 1995, pp. 5-34.
Livingstone, D. N., *Putting science in its place? geographies of scientific knowledge,* University of Chicago Press, 2003.

lace (in particular, zoogeography) and the growth of evolutionary theory based on Browne's *"The Secular Ark"* This book is considered a fundamental reference for biogeographical history researchers in the West.

Since the Age of Discovery in the 16th century, a great many living things were brought to Europe from the New World and overseas colonies. It therefore became clear that diverse varieties of organisms exist in various environments on the Earth, and this came to be viewed as being in contradiction with the contents of the Book of Genesis.

The first contradiction is the impossibility of accommodating an almost infinite variety of living things on Noah's Ark during the Deluge. Inconsistencies between the size of the Ark and methods of ensuring drinking water and food supplies arise.

The second contradiction is that Mt. Ararat (close to the Turkish-Armenian boarder) where Noah's Ark drifted ashore after the end of the Deluge and where disembarkation is considered to have commenced is an arid region. This begs the question of how the varieties of organism adapted to cold regions and humid tropics each safely migrated to their respective habitats.

Thus given, The Book of Genesis had already become thought to differ from reality in the 18th century. At length, multiple creationism, which considers organisms perfectly adapted to the environments of regions around the world to have been designed by the Creator many times over, began to spread. Multiple creationism became advocated and supported by many biologists[7].

Amongst them, the French natural historian Buffon (1707–1788) contended that as the respective regions of the world possessed diverse environments such as differing climates, the varieties of living creature developing there would also be diverse. Organisms supported by cold regions and warm humid regions would not survive in an arid climates such as that of Mt. Ararat. Therefore, Buffon assumed organisms were created by God at a given period when Europe was temperate and part of the old world, and asserted that descendants which could adapt to evergreen and deciduous forests dispersed and disseminated throughout the world thereafter[8].

At length a theory of evolution was assumed by the French Lamarck (1744–1829). Lamarck was not particularly concerned about the distribution of organisms but rather was greatly interested in the form of organisms and a system for their classification. Lamarck advocated the theory of used and disused organs, whereby continuously used organs subsequently develop and disused organs decline and remain as vestiges, and also a theory of heredity of acquired char-

7) Browne, J., *The secular ark: studies in the history of biogeography.* New Haven: Yale University Press, 1983.

8) Buffon, G. J. L., Buffons Natural History containing a theory of the earth, J. S. Barr, 1792.

acter. He claimed that the long neck of the giraffe was an example of an a posteriori acquired character inheritance that is advantageous for the eating of more leaves from the branches of taller trees. In other words, he extolled orthogenesis, by which organisms evolve in a prescribed direction determined in advance[9]. This theory of evolution had an influence on biologists to come however came to be refuted in the modern theory of biology.

In contrast, Cuvier (1769–1832), the French biologist and researcher into comparative anatomy and palaeontology, refuted Lamarck's evolutionary theory extolled a theory of catastrophe. Taking the differing of fossils according to stratification as an example, Cuvier claimed that catastrophes had repeatedly occurred throughout prehistory, on the occasion of which most of the living creatures of the previous geological age became extinct and new ones were created[10].

The British geologist Lyell (1797–1875) gave a rebuttal to the catastrophic theory of Cuvier. He published the first and second volumes of the *Principle of Geology*[11] from 1830–1833 in which he advocated a uniformitarian theory whereby all geological phenomena occurs currently as in the past by the same ongoing geomorphic agency and not by catastrophe. However at first, Lyell did not include the principle of the evolution of organisms in his uniformitarian theory. He considered evolution from one species to another to be impossible. He adopted a notion close to creationism whereby a completely new species is created after a species of living creature becomes unable to adapt to a changing environment and becomes extinct. At length he made exchanges with Darwin and Wallace and recognised the theory of evolution in the latter version of the *Principle of Geology.*

In the *Principle of Geology,* Lyell also indicated the effect of dispersal by fortuitous transport, the change of sea level, and continental upheaval and substance as causes of the distribution of living creatures and its expansion[12].

The above synopsis of Browne's masterpiece summarises the history of biogeographical theory prior to Darwin and Wallace, moving from a confirmation of global biodiversity and catastrophic theory to uniformitarian theory, from fixed species to evolutionary theory and furthermore from a linkage with natural theology to a general disaffection. Amongst all this, multiple creationism, which takes organisms as being repeatedly created in all locations was part of various attempts to integrate The Book of Genesis and the catastrophic theory, which were in the process of being refuted, with some kind of modern natural science[13].

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9) Lamarck, J. B., *Philosophie Zoologique,* Chez Dentu, 1809.
10) Cuvier, G., *Recherches sur les ossemens fossils de quadrupedes, ou Ton retablit les caracteres de plusiers especes danimaux que les revolutions du globe paroissent avoir détruites,* Chez Deterville, 1812.
11) LyelI, *Charles Principle of geology vol. I・II・HI,* John Murray, 1830–33.
12) op. cit., footnote 11) vol. II, pp. 66–122.
13) op. cit., footnote 7)

However the birth of Darwin and Wallace's theories newly extolling successive and branching divergence from a common progenitor in contrast to this kind of continuous multiple creationism, can be said to have been awaited with much anticipation. In other words in order to prove the continuous evolution of living creatures it was necessary to establish the distribution of related extinct plants and animals over a continuous period of time, or the spatial distribution of continuously related living creatures. Analysis concerning the cause of discontinuous distributions based on the existence of geographical barriers and geographical isolation was also necessary. In this way research into the distribution of organisms, namely research into biogeography, became an extremely important subject for the questions raised by modern evolutionary theory. Therefore, it cannot be ignored that there had already been this kind of flow of theoretical history as the setting for the evolutionary theories of Darwin and Wallace to be born and broadly socially accepted in the middle of the 19th century.

At the same time I would like to touch on the background for why the evolutionary theories of Darwin and Wallace were produced by Britons and came to be accepted primarily in Great Britain. The philosophy of the European Enlightenment, a modern rational science, was spreading throughout Great Britain during the 18th and 19th centuries. The construction of social infrastructures such as coal mining businesses, railroads, highways and canals was also vigorously underway due to the Industrial Revolution, resulting in cuttings being made into the ground everywhere and the exposure of geographical formations. As a result, the development of the resulting research into palaeontology and stratigraphy was linked with the important resources of coal mining and so was also of practical benefit to the industrial capitalists. This kind of development prompted further consideration for the historical evolution of living things[14].

Simultaneously, colonial expansion, the progress of foreign expeditions and development into a world empire accumulated a practical and aesthetic appreciation in the British people for the curious plants and animals overseas. The formation of an affluent leisured class in particular made possible the existence of amateur naturalists and specimen collectors. The part of the British government can also be identified in the dispatch of naval surgeons and colonial administrators, whose task it was to research biogeography at overseas locations, and the implementation of exploration voyages[15].

Furthermore, the spread of national education and the existence of various scientific societies such as the Royal Geographical Society can also be raised as institutional frameworks that contributed to this background. At the Royal geographical Society, the natural theological

14) Fichman, M., *Evolutionary theory and Victorian culture,* Humanity Books, 2002.
15) Browne, J., '*A science of empire:* British biogeography before Darwin', *Revue d'histoire des sciences,* 45, *1992, pp. 453. 475.*

providence of God was in decline and the study of the natural environment and geography of the colonies could be said to be becoming the main pillar of spiritual enlightenment[16].

This kind of social background in Great Britain can be identified as the basis of the formation of the evolutionary theories of Darwin and Wallace.

(2) Darwin's Biogeographical Discoveries and the Conception of Evolutionary Theory

As we have already seen, the existence of a British global ethos from the 18th to the 19th century such as the development of the European Enlightenment, the Industrial Revolution, and the expansion of the colonies is undeniably the basis of the social background for the establishment of evolutionary biogeography. Also research trends in biogeography since Darwin developed from creationism and catastrophic theory to uniformitarianism and gradualism together with a confirmation of global biodiversity. Together with the spread of the writings of this kind of biologist and geologist to society, information concerning the existence and distribution of diverse plants and animals from colonies around the world, and especially from the tropics, was brought back to Great Britain in the 19th century. As a result, the surprising diversity of species all over the world and the fact that species of organism differ according to location even if based in the same environment became evident. Because of this the correspondence between the environment and diverse organisms was confirmed not to be simple. This does not agree with creationism whereby species must have been created in perfect compatibility with the environment. Also catastrophic theory was considered to have been refuted by Lyell's uniformitarian theory. Meanwhile, multiple creationism whereby new species are created time and time again by the creator following the demise of a species due to sudden upheaval of environment came to be extolled by many biologists as resolving the inconsistencies of natural theology[17].

With these circumstances as a background, Darwin conceived the theory of evolution from the consideration of the distribution of living things. Darwin's interest in the geographical distribution of living things became a distrust of the fixation of species and the integrity of adaptation in creationism, and he came to study the concept that species is a hereditary derivative accompanying a change in form and the relativity and incompleteness of these adaptations. By means of the voyage of the Beagle, Darwin studied methods of species migration and migration barriers, the effects of isolation and adaptive radiation. Based on biogeographical data, Darwin understood that species are descendants from a common progenitor that have been modified

16) Livingstone, D. N., *The geographical tradition: episodes in the history of a contested enterprise,* Blackwell, 1992.

17) op. cit., footnote 7)

and changed in appearance and that the origin of a species was from a single central location from whence individuals migrated and became established[18].

Individuals of a species of the same genus are all separated from a central location with the same distribution and stem from the same ancestors of the same region[19].

Furthermore after his return to Great Britain inconsistencies between data such as the distribution of life-forms and fossils and creationism became evident, giving rise to the hypothesis of transmutation in 1837. This is to say that for Darwin, the faults with creationism were; ①the integrity of adaption, ②the direct relationship between species and the physical environment, ③the repeated creation in all locations and all periods of multiple creationism and ④catastrophic theory[20].

So specifically, what kind of conception did Darwin have from observations of what kind of organism?

① The Speciation and Distribution of Galapagos Island Finches and Mockingbirds

The following was understood as a result of the appraisal[21] of the bird specimens Darwin collected on the Galapagos Islands by Gould in 1837. Finches are birds that eat nuts, seeds and insects. Species of Finch with differing beak forms are distributed throughout the Galapagos Islands according to the distribution differing foods. Varieties of Mockingbird are also distributed such that they differ according to island.

If each species had been created here why had such an excess of species been created? Given the conditions and the locations of each of the volcanic islands of the Galapagos archipelago were approximately the same shouldn't each creature also be the same? Also why were the finches and hummingbirds of the Galapagos Islands similar to those of tropical America where the environmental conditions differed the most?

Darwin's solution with respect to these questions was as follows. The reason why the species were so similar was because they were descendants from a progenitor common to those distributed in the South American continent. Also, the slight change of form according to each island was the result of adaptive radiation to living patterns restricted to a specific island. The Creator had not worked a wonder for each island separately but rather separated populations had evolved so as to adapt to differences in the environment of each new island and gone on to be-

18) Richardson, A. R., 'Biogeography and the genesis of Darwin's ideas on transmutation', *Journal of History of Biology,* 14, 1981, pp. 1–41.

19) Darwin, C. R. *On the origin of species by means of natural selection or the preservation of favored races in the struggle for life.* John Murray, 1859, pp. 351–353.

20) op. cit., footnote 18)

21) Gould, J. (Darwin. C., ed.), *The zoology of the voyage of H. M. S. Beagle, Part III: birds.* Smith Elder and Co, 1841.

come a new species[22].

There was no great difference between the physical conditions of each island but rather there were differences in the competitive relationships of the organisms. Differing flora had been formed on each island and creatures migrating to the island afterwards competed with creatures that differed according to the island. Natural selection could be considered to have led to a more advantageous form of differing variety[23].

② The Distribution of Rodents and Rhea Native to Continental South America

The agouti and bizcacha, which are animals on the savanna of La Plata resembling rabbits, are similar to rodents peculiar to the American continent. Why is it they do not resemble those that inhabited the old world? The coypu and capybara of South America differ to the beaver and muskrat of North America. However irrespective of the diverse climate and environmental conditions of various places in South America the fauna are similar. There is no relation with fauna of places with equivalent climates and ecological conditions on other continents. This is not consistent with creationism. Also a small variety of ostrich (Rhea) lives in Patagonia, a larger variety of which inhabits the arid region of the South. This does not resemble the African ostrich or the Australian emu. Darwins solution was that these animals can be considered to have evolved from a common progenitor of South American origin[24].

This is to say that if the continent differs, the species of animal inhabiting varies greatly even if the environments are the same. Conversely, allied creatures are found to inhabit the same continent even if physical conditions differ[25].

③ The Fossils of Large Mammals Excavated in South America Resembling Smaller, Existing Species

Darwin excavated large fossils of the currently smaller species of sloth, armadillo and capybara on the prairie of La Plata[26].

Why do these deceased animals resemble animals currently alive? According to creationism, fossils should represent species made extinct by the Deluge of the Bible. As new species after the cataclysm must have been created to adapt to completely new environmental conditions by God, there should be absolutely no connection between fossils and species currently living.

22) op. cit., footnote 19) pp. 397-10.
Darwin, C. R. *Journal of researches into the geology and natural history of various countries visited during the Voyage of H. M. S. Beagle rounded by Charles Darwin,* John Murray, 1845, pp. 376-405.
23) op. cit., footnote 19) pp. 406-410
24) op. cit., footnote 19) pp. 349-350, and footnote 22) pp. 57-58, pp. 96-100.
25) op. cit., footnote 19) p. 349.
26) op. cit., footnote 22) pp. 88-91

Given that living species of creatures show a relatedness to extinct species, Darwin took the claims of catastrophists, whereby no descendants remain from species made extinct, to be refuted[27].

That is to say he became aware oi branching divergence from a common progenitor instead of the creation of species in adaption to particular environments by a Creator.

It is evident that all species of the same genus developed from the same place of origin[28].

Integrating the above knowledge, Darwin suggested that geographic isolation promotes geographic speciation. Geographical barriers are a necessary assistance to "natural selection". In natural selection, the creatures best adapted to an environment exist. Darwin thought that hybridization does not happen due to graphical isolation and adaption to the environment of a region, and infertility occurs.

At length Darwin noticed from research into barnacles the existence of diverse variations in the natural world even in the same environment. Darwin then began to stress sympatric speciation from geographic speciation. With regards to the principle of divergence, he began to think that creatures coexist in an ecological niche and sympatric speciation or branching divergence from a common progenitor occurs.

In the early days, Darwin stressed environmental change and geographical isolation as the main cause of evolution and speciation; however he later went on to stress random ecological divergence from a common progenitor. For Darwin, the significance held by geographic and environmental factors changed and the more ecological factors of the relationships between living things became important[29].

In this way, research asking in what way species are distributed throughout the world was important evidence facilitating Darwin's arrival at the theory of branching evolution from a common progenitor. The idea of divergence from a common progenitor was brought about by the process whereby populations adapt to physical or organic changes in the regional environment and as a result became the most persuasive argument for natural selection. Species are produced in a single location and undergo fortuitous transportation to other regions. Is the scattering of the same species over two or three locations separated by a great distance likely to be based on the multiple creation of parents of the same form? Darwin advocated dispersal from a single origin rather than multiple creation. The reason was that he thought discontinuous distributions occur due to the extinction of allied species in intermediate regions.

There are two important changes in Darwin's geographical way of thinking. One concerns

27) op. cit., footnote 19) pp. 312-345.
28) op. cit., footnote 19) p. 353.
29) Kottler, M. J., 'Charles Darwins biological species concept and theory of geographic speciation: the transmutation notebooks', *Analysis of Science,* 35, 1978, pp. 275-297.

the upheaval and subsidence of the Earth's crust on the geological time scale. The submergence of continents under the sea and the subsequent re-upheaval was thought to magnify speciation and distribution by means of geographical isolation and integration. Darwin considered that evolution and speciation is produced by the submergence of the Earth surface and fragmentation into islands, and that dispersal depends on the joining of land to facilitate migration. However after writing the *Origin of Species,* he started to consider that the arrangement of continents and oceans has had a permanence from the end of the Mesozoic era until present, and that there have been no great changes since.

The second change was the principle of divergence that accompanies sympatric speciation. Now the geographical isolation of islands is no longer important for the initial speciation. Speciation is occurring on the huge continental crust[30].

The population of an island is established by fortuitous migration from the mainland.

For example, seeds and nuts can be transported by ocean currents, migrate on driftwood or icebergs or be carried by birds in the alimentary canal, beak or claws[31].

However the restocking of form that occurs on the mainland cannot occur on islands and the island population is isolated, diverges by means of adaptive radiation and becomes a different species. Also these populations can only rarely spread to different islands. This cannot be explained by the viewpoint that each species is created independently. Only settlement from a close and ready origin and adaption to a new habitat can explain the resulting modification that occurs. The crossing of the equator by some species in accompaniment with a cooling of the northern hemisphere in the ice age and the subsequent relics which remain in the vicinity of high mountain summits is a similar phenomenon to "island populations"[32].

(3) Changes in the Concept of Geographic Speciation

Darwin read Malthu's, *Principle of Population* in October 1838[33]. The influence of this caused him to further stress intraspecies and interspecies competition more than geographic isolation as the main cause of the mutation of a species. Increase due to overproduction of a population intensifies competition. Slow changes in the physical environment do not directly lead to variation for the purpose of complete adaptation. Geographical barriers obstruct hybridisation and accomplish the role of assisting the effects of natural selection. Accordingly, rather than the

30) Bowler, P. J., 'Geographical distribution in the Origin of Species' (Ruse, M. and Robert, R. J. eds" *The Cambridge companion to the "Origin of Species",* Cambridge University Press, 2009), pp. 153-172.
31) op. cit., footnote 19) pp. 356-382.
32) op. cit., footnote 30)
33) Malthus, T. R., *An essay of on the principle of population: as it affects the future improvement of society, with remarks on the speculation of Mr. Gordon, M. Condorcet, and other writers,* J. Johnson, 1798.

cause of evolution, geographical distribution became used to verify the effects of when natural selection theory was in action. At that time the causes of variation such as polyploids and random genetic drift were not known however the explanation of random variation became indispensable to Darwin's theory. Darwin's interest then turned to the problem of adaptation of living things to the environment rather than the direct effect of the environment such as the formation of geographical barriers[34].

In short, Darwin thought that the most desirable species based on the struggle for existence are preserved and undesirable species become extinct. This result invites the formation of new species. That is to say an emphasis on competition more than that of geographic isolation was made in the theory of natural selection. In this manner Darwin came to accept the notion of sympatric speciation. This is partial isolation and ecological isolation.

Partial isolation is a cause whereby individual representative species are formed in a continuous continental region. In the case that adjoining ecological environments are nonidentical a fixed species decreases according to changes in physical conditions such as temperature or humidity and the habitat becomes restricted. Eventually a competitive species that can better adapt to the adjoining region becomes superior.

Ecological isolation is active at differing stations even within the same region such as though differences in breeding times etc., and occurs through crossbreeding between more similar individuals only. This can also be called reproductive isolation or behavioural isolation[35].

In other words Darwin noticed the need to consider the struggle for existence in natural selection based on the complex relationship between endemics and the regional environment rather than just on the limitations of environment and overproduction, also even if there is no geographical isolation, only the traits beneficial for adaption are preserved, and go on to develop and form new species based on hybridisation between diverse varieties over many years. Accordingly, geographical isolation supports the process of natural selection but is not a necessary condition for evolution[36].

For Darwin, the word "isolation" had two meanings. One meaning was the geographical separation that facilitates speciation. The other was the place where adaptive radiation became possible in a niche opening such as on islands isolated from large biota on the continent etc[37].

Orthogenetic evolution not related to geographical isolation and the ecological role of isolation then became emphasised in Darwin's *Natural Selection*[38]. A great number of variations are

34) op. cit., footnote 18)
35) Sulloway, F. J., 'Geographical isolation in Darwins thinking: the vicissitudes of a crucial idea', *Studies in History of Biology 3,* 1979, pp. 23-65.
36) Vorzimmer, P" 'Darwin's ecology and its influence upon his theory', *ISIS, 56,* 1965, pp. 148-155.
37) op. cit., footnote 35)

formed by divergence in homogenous regions that include diverse ecological niches[39].

The research[42] of Ospovat considered the transition in Darwin's concept of geographical speciation through comparing the 1844 manuscript[40] of *Essay* and the manuscript of *Natural Selection*[41]. published in 1856–1858. In the *Essay*[43] of 1844, it is not necessary for a species in a state of perfect adaption to the environment to change. Therefore the evolution of the species of creature occurs when the environment changes. That is to say variation slowly continues based on intermittent geological changes. Darwin also thought that species change significantly when geographic or climatic conditions change on a grand scale or when creatures suddenly migrate to a region to which they are not perfectly adapted.

However in 1856 Darwin further believed that the interrelationship of creatures within a fixed location was more important for evolution than external environmental conditions. In the sixth chapter of *Natural Selection*, Darwin claimed that an increase of variation and number of species can occur even if there is no geographical isolation or change in external conditions. That is to say divergence reduces to division of labour. Mutual relationships are more important than physical conditions for the existence of a living thing. Even if there are no differences in absolute environmental conditions due to geographical isolation, changes in organism and physical conditions must instead be taken relatively. Systems of mutual action and reaction between organisms and the actions of non-organic bodies invite diversity in the biological world. The adaption of living things is not strict and absolute but rather a plastic and flexible phenomenon. Changes in an organism occur independently of geological change and so whether or not the function of natural selection produces a new species depends on whether or not the location is open to the establishment of a new organism and whether or not the organisms of the region can be further diversified through the introduction of a new organism[44].

In Darwin's *Natural Selection* written from 1856 to 1858, variation was taken as a phenomenon that could occur at any time irrespective of change in exogenous or physical conditions. This meant the process of evolution was taken to be one of reciprocal action and reaction between organisms and to be independent of changes in external environment and physical con-

38) Stauffer, R. C. ed., *Charles Darwins Natural Selection: Being the second part of his big species book written from 1856 to 1858.* Cambridge: Cambridge University Press, 1975. The manuscript of Natural Selection had unpublished during Darwin's lifetime.
This manuscript has firstly been edited and published by Stauffer in 1975.

39) op. cit., footnote 35)

40) Darwin, C., 'Essay of 1844s (Darwin, C.. and Wallace, A. R., *Evolution by natural selection, The Syndics of* The Cambridge University Press, 1958) pp. 91–254.

41) op. cit., footnote 38)

42) Ospovat, D., *The development of Darwin's theory: natural history, natural theology, and natural selection, 1838–1859,* Cambridge University Press, 1981, pp. 170–209.

43) op. cit., footnote 38)

44) op. cit., footnote 42)

ditions. Accordingly, the concept noted in Darwin's *Essay* of 1844 whereby an organism perfectly adapts to the environment and evolution takes place was removed.

It is conceivable that there were two reasons for Darwin's notions concerning variation to change in this manner. The first is that Darwin believed large variations in large genera did not depend on changes in external conditions. Instead he noticed that variations are based on the characteristics of large genera. Secondly he noticed that there is the possibility for creatures to diversify and change even under almost uniform conditions. Namely, variation arises at any time due to slight changes in circumstance such as cold winters, dry summers or the entry of a new organism. Furthermore Darwin also stopped distinguishing and considering slight differences and large variations between individuals.

The existence of a competitor or the pressure of an increase in population further advances adaption through ecological specialisation and division of labour within the group, and forms diversity. The group is further improved by this kind of diversity. Viewed from this kind of perspective adaptation became a relative concept in natural selection[45].

Above all is the importance of Darwin's research into the relationship between botanical arithmetic and the principle of divergence in 1855. with this Darwin confirmed the correlation between species and variety and the number genera and, including that the number of mutations become greater than average in large genera, attempted to clarify the relationship between the great number of forms such as initial species and closely allied species etc. this spreads as wide as the large group of the natural world. Representative species geographically and mutually excluding each other gradually disseminate to a larger region, meet different conditions, and upon achieving adaption to the region form taxonomically related allied species. If there are many representative species in a genus, then the scale of the group becomes even larger in comparison to the geographical sphere. Then large genera widely disseminate and tend to further change. Even if the natural conditions change and the genus is isolated from the remaining group it has an even greater ability to adapt and can exist for even longer.

In this way geographical isolation was necessary in Darwin's picture of evolution but went on to become remarkably different. In other words, this relates to a process whereby new genera are produced from old genera, giving rise to the necessity of the role of divergence and competition and maintenance of an appropriate niche. For Darwin it was conceivable that even more compatible species could occupy that kind of niche. Accordingly and by means of research into botanical arithmetic, Darwin attempted to clarify that the more diverse a large genus is, the greater the number of species produced[46].

45) op. cit., footnote 42)

46) Browne, J., 'Darwin's botanical arithmetic and the "Principle of Divergence," 1854–1858', *Journal of*

III Biogeographical Considerations and Concepts of Evolutionary Theory According to Wallace

On an expedition to the Amazon, Wallace made the discovery that although closely related, the species on the banks of the geographical barrier, the Amazon River, differed from those on the opposite bank. Wallace believed that this was because they originated from the same species, were isolated by the barrier and subsequently came to evolve over time. Wallace, who furthermore developed this idea, wrote a thesis in Borneo in 1855 and announced the theory that "Every species has come into existence coincided both in space and time with pre-existing closely allied species". That is to say he advocated an evolution that was temporally and spatially continuous rather than an intermittent creation[47].

The foundation of Wallace's biogeography was the integration of geological and climatological data such as the effect of glaciers and changes of sea level on the premise that the arrangement of continents and oceans was basically permanent. The concepts of migration pattern and the dispersion of living things, and evolutionary adaption and divergence were integrated as guidelines for his research. In this way Wallace's notion of evolutionary theory stressed the geographical distribution of living things and the impact of the environment more than Darwin[48].

Wallace established zoogeographical regions for the world on a macroscopic level based on a global permanence of land and sea arrangement[49]. However in the explanation for peripheral sections such as islands and the boundaries of these regions the impact of the upheaval and subsidence of the Earth's crust, the effect of glaciers and changes of sea level continued to be stressed[50].

Also, Wallace's line, which Wallace discovered in the Malay Islands was not just a boundary

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History of Biology, 13, 1980, pp. 53.89.

47) Wallace, A. R., 'On the law which has regulated the introduction of new species', *Annals and Magazines of Natural History,* 16, 1855, pp. 184–196.

48) Smith, C. H., *Alfred Russel Wallace- an anthology of his shorter writings,* Oxford University Press, 1991.

49) Wallace, A. R., 'On some anomalies in zoological and botanical geography', *Natural History Review,* 4, 1864, pp. 111–123.
Wallace, A. R., *The geographical distribution of animals vol. I–II,* Macmillan & Co., 1876.
Wallace, A. R., *Tropical nature and other essays, Macmillan & Co.,* 1878.
Wallace, A. R., *Island life or, the phenomena and causes of insular fauna and floras, including a revision and attempted solution of the geological climates.* Macmillan & Co., 1880.

50) Wallace, A. R., 'On the Arru Islands', *Proceedings of the Royal Geographical Society,* 2–3, 1858, pp. 163–171.
Wallace, A. R 'On the zoological geography of the Malay Archipelago', *Journal of the Proceedings of the Linnean Society Zoology, 4, 1860,* pp. 172–184.
Wallace, A. R 'On the physical geography of the Malay Archipelago,, *The Journal of the Royal Geographical Society, 33, 1863,* pp. 217–234.

of fauna for the Australian and Oriental region, but is also viewed as the location where the Australian continental plate is subducing with the colliding Eurasian plate according to the plate tectonics theory of today[51].

Let's look at the formation process of Wallace's biogeographical evolutionary theory in a little more detail. Wallace led a frugal life and then from 1848 to 1852 went on an expedition to South America. It was his plan to live in South America where living expenses are cheap, sell the specimens he collected in South America in Great Britain in order to raise travel expenses, acquire capital and pursue research into his passion of natural history. At length Wallace observed the distribution of palms, birds, insects and monkeys whilst collecting specimens. The environment of both banks of the river was the same but the species on each bank, although closely related, were different. In the old high lands, the woodlands and on the alluvial plains, the butterflies, umbrella birds and palm trees on both banks of the river were mutually related but distinct allied species[52]. Why would an omnipotent God have created different species on each bank of the river? Instead, is it not likely that evolution had formed a new species which separated from the parent species after the geographical barrier was established?

Wallace specifically classified the distribution of life-forms by the various regions of Guiana, Ecuador, equatorial Peru and Brazil together with separating them according to both banks of the Amazon, Negro, and Madeira. White and grey tamarins are distributed on the north bank of the Amazon River and the east bank of the Negro River in Guiana. The woolley-monkey is distributed in the Amazon basin and the generally corpulent monkey in Peru. These are not found on the east bank of the Negro River. The yellow-handed howling monkey is distributed in the vicinity of Para (Belem), and the Negro Tamarind on the south bank of the Amazon. Similarly, the geographical distribution of many birds, insects and monkeys is restricted. On the opposite bank of the geographical barrier, slightly differing species of an intimate relation are found. This is because they originated from the same stock, with each section coming to evolve over time[53].

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51) Audley-Charles, M. G., Hurley, A. M., and Smith, A. G., 'Continental movements in the Mesozoic and Cenozoic' (Whitmore, T. C. ed., *Wallaces line and plate tectonics,* Clarendon Press, 1981), pp. 9–24.
Audley-Charles, M. G., 'Geological history of the region of Wallace's line' (Whitmore, T. C. ed., *Wallace's line and plate tectonics,* Clarendon Press, 1981), pp. 24.35.
Oosterzee, P. V. *Where worlds collide: the Wallace Line,* Cornell University Press, 1997. Hayami, I., 'Geohistorical background of Wallace's line and Jurassic marine biogeography' (Taira, A. and Tashiro, M. eds., Historical biogeography and plate tectonic evolution of Japan and Eastern Asia, Terra Scientific, 1987), pp. 111–133.

52) Brooks, J. L., *Just before the origin: Alfred Russel Wallace's theory of evolution,* Columbia University Press, 1984.

53) McKinney, L. H., *Wallace and natural selection,* Yale University Press, 1972. McKinney, L. H., 'Alfred Russel Wallace and the discovery of natural selection', *Journal of the History of Medicine and Allied Sciences, 22,* 1966, pp. 333–357.

The frequent existence of precise boundary lines of distribution irrespective of the fact that they can be easily crossed by birds and insects was a most important discovery in Amazon field research. For example, part of the common progenitor stock crossed the barrier of the river by chance, giving rise to migration and becoming the basis of the current variation. Continuous variation exceeding this kind of time period resulted in the formation of differing species[54].

However Wallace's valuable specimens and observation records from the Amazon over this four-year period were mostly lost in a ship fire on the Atlantic Ocean during his return to Great Britain in 1852.

Without being discouraged by this misfortune Wallace made an application for support to the Royal Geographic Society upon his return to Great Britain and made a further research expedition to the Malay Islands over the years 1854 to 1862. the reason the Malay Islands were selected as a destination is said to be because Wallace wanted to clarify the way in which the diverse biota of the tropics were distributed on the islands according to the barrier of the ocean. It can be assumed that this was because he was influenced by the descriptions of the Galapagos Islands from Darwin's the *Voyage of Beagle,* already published[55].

On the journey he wrote and announced the thesis "On the Law which has regulated the introduction of new species" on Borneo island in 1855 (currently Kuching, Sarawak, Malaysia)[56]. This was the seed of Wallace's theory of evolution which is generally called the Sarawak Law.

Before entering into these details we must touch on the research of Forbes, who influenced Wallace's writing of the Sarawak Law. Forbes made attempts to integrate the distribution pattern of fossils and that of living creatures. He introduced concepts based on the upheaval and subsidence of the Earth's crust and the change of sea level due to glacial variations into the methodology of biogeography, and tried to petrogenetically explain the continuing changes in the distribution of life-forms from the past to present[57]. However he was very much a creationist and teleologist. In 1854 he extolled the "theory of polarity", he claimed that the scheme of creation as ordered by God is such that types of genus continue to develop the most with regards a to polarity within time in a natural system. Accordingly a temporal and spatial arrangement of polarity is taken in order to balance mutual extremes. Therefore fossils are abundant in the old initial period and the newer period and are scarce in the interim. The world of organ-

54) Fichman, M., *An elusive Victorian- the evolution of Alfred Russel Wallace,* The University of Chicago Press, 2004.

55) Smith, C. H., 'Alfred Russel Wallace 1823-1913' (Freeman, T. W. ed. *Geographers biobibliographical Studies volume* 8, Mansell Publishing, 1984), pp. 125-133.

56) op, cit., footnote 47)

57) Forbes, E., 'On the connexion between the distribution of the existing fauna and flora of the British Isles, and geological changes which have affected their area, especially during the epoch of the northern drift', *Memoires of the Geological Survey of Great Britain, 1,* 1846, pp. 336-432.

isms goes on to resemble the world of non-organic bodies through the expression of a force which attempts to develop towards one of two poles, which are an ideal condition. Hence the various forces of development are particularly intense in the oldest and the newest geological ages. Forbes therefore claimed that most genera were formed in the Palaeozoic and Cenozoic eras rather than the Mesozoic era[58].

In contrast, Wallace read Lyell's *Principle of Geology*[59], came to refute the catastrophic theory, and was convinced from his observations of the distribution of life-forms in the Amazon that creatures isolated by a geographical barrier undergo branching divergence from a common progenitor. He could not approve of a theory of the intermittent and isolated evolution of creatures such as that of Forbes. The claim that "Every species has come into existence coincided both in space and time with a pre-existing allied species^, which is the idea behind the Sarawak Law was brought about in this way[60].

In this manner Wallace's Sarawak Law was the application of the uniformitarian theory[61] of Lyell's *Principle of Geology,* which takes geological change to be continuous in the long term, to the changes of organisms. However at that time, Lyell did not recognise the continuous evolution of creatures and considered species to become extinct due to environmental changes with new discrete species created independently. Refuting this also, Wallace advocated his Sarawak Law as a theoretical law to explain the distribution of living creatures on the Earth both in the past and in the present. This stated that closely allied species precede existing species in both evolution, which carries the continuity of species, and in the natural world[62].

However although the Sarawak Law was a theory that explained the temporal and spatial distribution of species, it did not give any explanation concerning the essential mechanisms for the evolution of the species. Wallace's speculation concerning the mechanisms of evolution continued. Notes of Wallace's speculations from 1855 to 1859 are preserved at the London Linnean Society. Lyell's theory is continuously cited within them, with consideration given to the organisation of arguments relating to evolution, proof of evolutionary design, theories of gradual development, evolution and speciation, geographical variation and gaps in fossil records. These details are quoted and viewed by Beddall[63] however a summary of the sections from within those notes, particularly concerning the relationship between species and variety, is as follows.

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58) Forbes, E., 'On the manifestation of polarity in the distribution of organized being in time', *Notices of the proceedings of the Royal Institution of Great Britain,* 1, 1854, pp. 428–433.
59) op. cit., footnote 11)
60) op, cit., footnote 47)
61) op. cit., footnote 11)
62) Beddall, B. G., 'Wallace, Darwin, and the theory of natural selection' A study in the development of ideas and attitudes., *Journal of History of Biology,* 1, 1968, pp. 261–323.
63) op. cit., footnote 62)

"If one species of plant on a continent is dispersed to distant locations, variety arises at each location due to differing soil and nutrient conditions. As they are separated over a long distance there is no cross-fertilisation of either variety. These finally become permanent species and now can no longer cross-fertilise."

"To say that that geographic varieties have permanent characteristics is a contradiction however if varieties do have permanent characteristics and only differ by a subtle variation, this becomes a graded difference and drawing a line separating both becomes difficult." In short Wallace tried to clarify the relation between the permanence and non-permanence of variety through graded difference.

The essentials of the "Note on theory of permanent and geographical varieties"[64] announced by Wallace in 1858 can be summarised as follows. If segmented geographical distributions and species of differing form are discovered in succession then it can be thought that species and variety are only distinguished by criterion. Is it likely that a Creator would be responsible for this kind of fine distinction? These are all descendants that have evolved from a common progenitor. Consequently the concept of "specially created unvarying species" and "permanent varieties" that arise due to evolution cannot coexist.

During this period interest particularly gathered concerning the variation and distribution of bird-wing butterflies (*Onithoptera*) in the Malay Islands. From the consideration of the diversification of subspecies, the impact of geographical isolation, and the extinction of migrating species of intermediate form, these varieties became the seed of the notion of evolution into independent species for which the variety accompanying geographic variation has permanence[65].

In this way Wallace, who had been troubled by the connection between evolution and geographical and ecological distribution, and the relationship between the change of organisms and adaption to the environment finally conceived of the theory of natural selection from Malthus' *Principle of Population*[66] as a theory to determine the trends of change. The essay "On the tendency to depart indefinitely from the original type"[67] that Wallace wrote in 1858 is taken to have been written in Ternate and so is generally called the Ternate Law. This claims that from within the varieties, typical populations likely to adapt well to an environment and survive are likely to evolve. Namely, a continuous variety that will survive for a long period is pro-

64) Wallace, A. R, 'Note on the theory of permanent and geographical varieties', *The Zoologist, 16*, 1858, pp. 5887-5888.

65) Wallace, A. R., 'On the phenomena of variation and geographical distribution as illustrated by the Papilionidae of Malayan region, *Transactions of the Linnean Society,* 25, 1865, pp. 1-71. op. cit" footnote 50) pp. 84-93

66) op. cit., footnote 33)

67) Wallace, A. R., 'On the tendency of varieties to depart indefinitely from the original type', *Journal of the Proceedings of Linnean Society Zoology, 3, 1858*, pp. 53-62.

duced by a parent species from within many varieties, and goes on to further separate from the original type. In the struggle for existence, a countless number of creatures are borne and resources for life are limited. Accordingly species equipped to avoid insufficiency of food supply or becoming the prey of enemies evolve and go on to multiply at the sacrifice of species that could not adapt.

IV Differences in the Evolutionary Theory of Darwin and Wallace

Wallace held a lifelong opposition to the notion of the heredity of acquired characteristics acquired a posteriori, however Darwin temporarily and partially gave acknowledgement to a heredity of acquired characteristic. According to Nicholson, in contrast to Darwin's stressing competitive selection, Wallace placed importance on environmental selection[68]. In other words according to Bowler, the difference was that Darwin stressed natural selection due to differences in individuals whereas Wallace placed importance on natural selection due to the existence and continuation of variety[69].

Bulmer points out that Wallace's Ternate Law considers inferior varieties under pressure of annihilation by further environmental deterioration to coexist with other excellent varieties. Namely, the Ternate Law becomes the expansion of the following kind of logic. Shortage or abundance for a population of a species is connected with the organisation and habits of the species. Species that cannot adapt go on to become scarcer than species that adapt well. Furthermore, if physical conditions deteriorate excellent varieties go on to replace the position of the former species. Varieties that can better adapt become prominent and continuous evolution and divergence arises, accordingly more adapted varieties become greater in number than varieties not adapted and related varieties depending on the same resources can coexist, even if only temporarily. If environmental conditions deteriorate, the pressure on both varieties is increased. However the varieties few in number which are not so well adapted are the first to perish. The continuation of this process shows the trend to depart from an initial type towards an infinite variety. In conclusion, Bulmer claims that Wallace does not allude to "ecological competition between sympatric individuals". which is the essence of Darwin's principle of divergence[70].

Furthermore according to Kottler, the principle of divergence in Darwin's *Origin of Species*

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68) Nicholson, A. J., The role of population dynamics in natural selection, (Tax, S. ed. *Evolution after Darwin, Vol. I The evolution of life,* The University of Chicago Press, 1960), pp. 477–521.

69) Bowler, P. J., 'Alfred Russel Wallace's concepts of variation,, *Journal of History of Medicine and Allied Sciences, 1976*; 31': pp 17–29.

70) Bulmer, M., The theory of natural selection of Alfred Russel Wallce FRS. J, *Notes and Records of the Royal Society,* 59, 2005, pp. 125–136.

is broader than that of Wallace and contains both divergent phyletic (linear) evolution and divergent branching evolution. Meanwhile, he identified that although Wallace's Sarawak Law alludes to branching evolution, the Ternate Law only alludes to phyletic evolution. However branching evolution and adaptive radiation is also a reflection of the advantage of biological diversity. The reason for this is diversity relieves the competition between various coexisting forms. The idea of this diversity was not fully recognised by Wallace until the publication of Darwin's Origin of Species in 1859. This was quite natural as Wallace stressed environmental selection rather than a Darwinian competitive selection[71)]

Also, Bowler develops the following point of argument concerning the differences between the concepts of Darwin and Wallace's variation and notion of selection. Darwin says that the struggle for existence initially arises from individual differences in the same species. The result supports the formation of variation that is a population that has an advantageous characteristic. Simultaneously, species are dependent on differing geographic conditions. Permanent variations well adapted to these conditions and well characterised are brought forth according to the effects of geographical isolation and natural selection. Furthermore as a second stage, well adapted variations survive and variations that cannot adapt are destroyed and are lost due to the competition between variations. Thus natural selection further transforms variation into species. Only this latter part of Darwin's theory is discussed in Wallace's Ternate Law. There is a greater interest in the existence of variation than in that of the individual, and the mutual competition between variations and the resulting formation of a new variation is taken up. There is no reference to the process by which permanent variations are actually formed by means of the effect of natural selection on the subtle differences ot the various individuals. The subject of the argument concerns differing groups within the species, not individuals. In short, the first stage of Darwin's theory is considered to be natural selection between various individuals after which natural selection is carried out between variations as a second stage. This means that Wallace only considers the second stage[72)].

Also according to Nicholson, Darwin's competitive selection is the replacement of incompatible forms and the preservation of more compatible ones whereas Wallace's environmental selection is the direct removal of incompatible ones. Environmental selection is a hard selection, the external environment is the absolute criterion and individual organisms are in conflict with this external environment. The continuance of a species is based on the direct relationship with the external environment and not the characteristics of individuals within the species. Mean-

71) Kottler, M. J" 'Charles Darwin and Alfred Russel Wallace: two decades of debate over natural selection (Kohn, D. ed. The Darwin Heritage, Princeton University Press, 1985), pp. 367-432.
72) op. cit., footnote 69)

while Darwin's competitive selection is a direct reciprocal selection between the individuals of the same species, with Darwin believing that variations in the external physical environment were not entirely necessary for evolution. On the other hand Wallace's environmental selection is determined by the congenital strength of resistance against adversarial environmental factors. It is not determined by the improved characteristics of bions. However in reality, the improvement of a selected creatures essential qualities does not mean it was entirely determined by the strength of natural or adversarial factors. This in turn means changes in the course of evolution are driven by accidental genetic variation, which comes from being one potential factor of selection. In soft competitive selection, individuals of the same species compete with regards to limited resources however if excellent variations do not exist, inferior variations can also continue to exist, whereas in hard in environmental selection individual species and variations complete against environmental deterioration, and only those resilient to the change in environment survive irrespective of the various characters of the individuals of the same species. Inferior species can also temporarily coexist due to the deterioration of environment but are finally destroyed in the end[73].

As we have come to see above, Wallace emphasised the group of organisms called a species or genus more than bionts whereas Darwin emphasised the individual and depicted a structure of individuals in detail. Fagan stated the following concerning the social background of the differences in practice of these two naturalists. Wallace was a pioneer of physical geography who, by means of the prolonged intensive collection of a large quantity of samples, immersed himself in a complete cataloguing of different species distributed throughout many regions. Darwin sporadically alighted on diverse locations on the itinerary of his voyage on the Beagle, carried out long and meticulous gathering activities and made detailed observations of new and interesting individuals. Although Darwin was restricted by the Beagled itinerary for the reconnaissance survey of the coast he was a member of a kind of wealthy leisured class and had almost no official obligations or economic constraints. Meanwhile Wallace was financially poor and had to collect and create a large number of specimens for his livelihood. On the other hand, as a freelance specimen collector Wallace could freely put together his schedule for his expeditions. It was probably for this reason that Wallace intently grasped the features of the regional fauna only rather than making a detailed observation of individual variations. This kind of difference exists as the background to the characteristics of the research[74].

73) op. cit., footnote 68)

74) Fagan, M. B., 'Wallace, Darwin, and the practice of natural history', *Journal of History of Biology,* 40, 2007, pp. 601–635.

V Conclusion

Whilst creationism was being refuted in the 19th century, the elucidation of the process of dispersal and divergence from a common progenitor in one original place was required in order to establish the successive temporal and spatial evolution of living things. The direction of research into this kind of biogeography of the distribution of living things concurred with the biological paradigm shift that was the proposal of evolutionary theory.

Initially, Darwin thought that the individual variations of living things were caused by exposure to a new environment and that new species were produced by the geographical isolation of these living things. "Geographical isolation" was taken to be important as a principal component of this speciation and research into the migration and diffusion of living things was conducted. The change of sea level and the enlargement and reduction of continents were considered as causes of this geographical isolation. However Darwin later came to reject this "hypothesis of a land bridge". That is to say Darwin thought that given sufficient time, and physical and ecological barriers are removed; a species will spread throughout the world. Darwin initially considered the impact of a change of geographical barrier with regards to speciation however he came to stress the mechanism of fortuitous transport such as adhesion to driftwood or animals, transport inside the alimentary canal and the effect of wind and ocean currents as the cause of this diffusion and geographical distribution. Hence the primary factor of structural change of the surface of the Earth became unnecessary in explaining distribution patterns. Furthermore through carrying out observations and research into particles after his return to Great Britain, Darwin understood the large quantity of variation in the natural world even in identical environments. In short, the variation of living things occurs even without geographical or geological change[75].

Meanwhile in contrast to Darwin, Wallace spent his life considering the relationship between evolution and geographical distribution in his theory, and continued to explain the influence changes in the geographical factors of the environment have on the distribution of living things and evolution[76]. In his paper concerning the Malay Islands, he stresses changes in the Earth's crust such as upheaval and subsidence as impacts had on the distribution and isolation of living things. In the writings of Wallace after his return to Great Britain, the effect of glaciers and the change of sea level are stressed more than changes in the Earth's crust as the primary geographical factors influencing the distribution of living things[77]. Could this change not be viewed

75) op. cit., footnote 30)
76) Nojiri, W., Distribution boundary, and evolution－Alfred Russel Wallace's biogeographic theory, *Japanese Journal of Human Geography* 6, 2009, pp. 293-311.
77) op. cit., footnote 50)

as being influenced by the above changes in Darwin's theory? In short Wallace established a worldwide zoogeographical region based on the permanence of a global distribution of land and sea at a macroscopic level. However he continued to stress the impact of changes in the Earth's crust and in glaciers and sea levels on the microscopic regional scale of peripheral sections such as boundaries and islands[78].

This is also reflected in the differences between Darwins and Wallace's theories of evolution. In Darwin's *Origin of Species,* the main constituent of evolution is very much the bion. An individual in a species occupies various positions and locations in connecting with the ecosystem, the individual proactively adapts to those conditions and variation is produced. At length, the variation of each individual accumulates average, the whole species diverges and new species are formed[79]. In contrast, Wallace's evolutionary theory as shown by the Ternate Law states that the unit of evolution is variation; only variations to adapt to changes in environmental conditions such as ensuring a food supply occur; and these evolve into a new independent species[80].

When compared with Darwin in this way, Wallace's theory of evolution places extreme importance on environmental change and geographical distribution. In other words might it not be possible that upon his return to Great Britain Wallace called himself a geographer and by means of this claim attempted coexistence with and differentiation from Darwin's theory of evolution?

This is to say, Darwin's theory of evolution recognised the diversity of the random changes of many individuals. This is also the reason why Darwin's evolutionary theory has not become obsolete in relation to the later development of biology in the 20th century, and the discoveries of hereditary mechanisms, polyploids and random genetic drift.

Thereafter, Darwin's theory of evolution was introduced to Germany by Haeckel and started to spread. Biogeographical and ecological theory came to be introduced to geography by Ratzel who was strongly influenced by Haeckel[81].

Incidentally, Haeckel is famous in biological history as the originator of the word "ecology" and for the claim "Ontogeny recapitulates phylogeny". The latter expression asserts that changes of form or structure in the process of gametogenesis for an individual living thing follows the change in form from microbe to a higher form of life. In other words it can be thought that the eternal evolution of living things can be elucidated from the analysis of the processes of reproduction and ontogeny in addition to the analysis of fossils. In this way Haeckel's con-

78) op. cit., footnote 48～49)
79) op. cit., footnote 19)
80) op. cit., footnote 67)
81) op. cit., footnote 2)

cept differed to that of Darwin in that it depended on orthogenesis. Also, although the biology of Haeckel broke down the concept of natural theology in Germany, it was on the other hand, an organic monism that was strongly influenced by the ideology of romanticism[82]. The geography of Ratzel, which received this kind of ideology from Haeckel, can be thought to be inclined towards a holistic theory of social organism[83].

It is therefore necessary to read and comprehend German literature in detail concerning the processes into which Darwin's ideology was introduced to German geography and furthermore 20th-century geography thereafter by the intermediaries of Ratzel and Haeckel as a biogeographical and ecological methodology that differed to its initial meaning. I would like to undertake this task hereafter.

Note: I would like to dedicate this paper to Dr. Toshio Matunaga (Emeritus Professor, St. Andres University) from whom I received advice concerning the history of biology.

(Accepted on 16 November, 2020)

82) Kelly, A., *The descent of Darwin—the popularization of Darwinism in Germany, 1860-1914,* The University of North Carolina Press, 1981, pp. 10-36.

83) Peet, R., The social origins of environmental determinism', *Annals of the Association of American Geographers, 75, 1985,* pp. 309-333.