Darwin's Hypotheses on the Origin of Domestic Animals and the History of German Shepherd Dogs

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Abstract. Charles Darwin devoted the first chapter of his book *On the Origin of Species* (1859) to the principles and products of artificial selection and concluded that this process is analogous to natural selection in the wild. With respect to the origin of the domestic dog (*Canis familiaris*), Darwin suggested that several canid species provided ancient founder populations for this phenotypically diverse mammal. In contrast to Darwin, the geologist Charles Lyell argued in 1859, with reference to the work of the zoologist Thomas Bell, that all breeds of the domestic dog are derived from one species, the grey wolf (*Canis lupus*). In this article we show that Darwin's analogy between artificial and natural selection was correct: domestication involves large, heritable phenotypic changes in an animal species over many subsequent generations and hence represents a rapid evolutionary process. We deduce the "Bell-Lyell" hypothesis and document that the grey wolf is indeed the immediate ancestor of the domestic dog. In his book on the *Expression of the Emotions in Man and Animals*, Darwin (1872) described the behaviour of a half-bred German Shepherd. Based on these observations, we summarize the history of this new breed of dog that originated in 1899. We conclude that quantitative data on body mass and other parameters, documented in a series of breeding records published between 1922 and 2002, may yield insights into the dynamics of this ongoing microevolutionary process.

1 Introduction

In June 1858, the botanist Joseph Hooker (1817–1911) and the geologist Charles Lyell (1797–1875) communicated two short manuscripts to the *Linnean Society of*

London, which dealt with similar subjects, i.e., the struggle for existence (or life) in natural populations of organisms that may result, over thousands of subsequent generations, in the transmutation of species. These "Darwin-Wallace"-papers, which were read on July 1st 1858 in the absence of the authors, were both inspired by a book of Robert Malthus (1766–1834) on the growth of human populations with respect to limited resources. Charles Darwin (1809–1882) was working on a long manuscript entitled "Natural Selection". This work was more than two-thirds complete when he received a letter from Alfred Russell Wallace (1823–1913). On these pages, which became known as the "Ternate-Essay", the struggle for existence in populations of free-living animals was described in detail. However, Darwin's key-term, "natural selection", was not mentioned in this short manuscript of Wallace.

In his sections of the joint article that was published a few weeks later, Darwin (1858) described the results of artificial selection by man and concluded that this has been the main agent in the production of domestic races of animals such as

Fig. 1 The association between humans and canids. During the first half of the 19th century, domestic dogs of unspecified breed were used throughout Europe by poor people as "work horses" (adapted from an anonymous drawing, ca. 1846).

sheep and cattle. A comparative analysis of the classic Darwin-Wallace-publications revealed that, according to Darwin (but not in the opinion of Wallace 1858), the analogy between artificial and natural selection was of central importance, notably in Darwin's subsequent 1859-book *On the Origin of Species* (Kutschera 2003, 2008; Smith and Beccaloni 2008).

In this article we describe and analyze Darwin's concepts on animal breeding with special reference to the evolution and domestication of the dog (Fig.1).

2 Pigeons and dogs: Darwin versus Lyell

In the first Chapter of his book *On the Origin of Species* (1859), Darwin described the variation in populations of domestic animals and plants. In the middle of this chapter, he argued that it is best to study some special group of organisms and therefore decided to focus on domestic pigeons. To become familiar with these animals, Darwin bought and kept on his farm-estate home at Down, southeast of London, every British breed available at that time. Fifteen domestic varieties that fanciers had "created" by selective breeding were cultivated in a dovecote at Down. Based on his observations and results from foreign sources, Darwin (1859) concluded that the common opinion of the naturalists of his time was correct, namely, that all these varieties have descended from one free-living species, the rock pigeon (*Columbia livia*). In his subsequent monograph on *The Variation of Animals and Plants under Domestication*, Darwin (1868) provided more detailed evidence for his general conclusions (Fig. 2).

*Fig. 2 Varieties of domestic pigeons that differ significantly with respect to their morphology, colour and behaviour. Charles Darwin's conclusion that all breeds descended, with modification, as a result of artificial selection from the free-living rock pigeon (*Columbia livia*) has been confirmed by subsequent investigators (adapted from Darwin 1868).*

Today we know that Darwin's hypothesis on the origin of domestic pigeons was correct (Daniel 2008). Moreover, the author of this article provided facts to support the theory that feral pigeons (*Columbia livia*), the free-living descendants of artificially selected, domesticated rock-pigeons, represent the re-constituted wild

phenotype of this taxon. In addition, Daniel (2008) summarized data indicating that natural selection, i.e., the exposition of the domesticated variety to their ancestral selective pressure, may be the process that led to the rapid re-occurrence of the "wild" phenotype in populations of free-living feral pigeons. However, more work is required to further test this hypothesis.

With respect to the domestic dog (*Canis familiaris*), the British naturalist suggested that "several wild species of Canidae have been tamed and that their blood, in some cases mingled together, flows in the veins of our domestic breeds" (Darwin 1859, p.10). In contrast to his conclusions as to the origin of domestic pigeons, in this case Darwin (1859) did not take into account the opinions of his most prominent peers. In an important monograph on British vertebrates by Thomas Bell (1782–1880), the zoologist who investigated and described reptiles that Darwin had collected during his voyage with the Beagle (1831–1836), facts that point to another hypothesis are summarized as follows: "… the Dog and Wolf will readily breed together, and their progeny is fertile … A point of considerable importance in the question of identity of species is the period of gestation. This circumstance is so invariable in individuals of the same species, and so rarely the same in those which are distinct … the (gestation) period of the Jackal is fifty-nine days, whilst that of the Wolf is sixty-three days, the same as that of the common Dog" (Bell 1837, p.197–198).

One of Darwin's mentors and friends, Charles Lyell, referred to Bell's opinion quoted above and to Bell's hypothesis that "all the various races of dogs have descended from one common stock, of which the wolf is the original source". The famous author of a classic textbook on Geology (Lyell 1830–1833) tried to convince the author of the *On the Origin of Species* that this assumption should be mentioned in Darwin's book: "The admission which I least like among your familiar illustrations is that while the various pigeons have descended from one stock the dogs have come from two or more species" (Letter, 21. Nov.1859, Charles Lyell to Darwin, DaCoPro 2008). In the first edition of the *Origin of Species* (1859), Darwin wrote "I do not believe, … , that all our dogs have descended from any one wild species" (Darwin 1859, p. 17). In the second and all subsequent editions, this sentence was enlarged as follows: "I do not believe … that the whole amount of difference between the several breeds of the dog has been produced under domestication; I believe that some small part of the difference is due to their being descended from distinct species" (Darwin 1872a, p. 31).

Today we know that wolves (*Canis lupus*) are the ancestors of all domestic dogs, which are assigned to a separate species (*Canis familiaris*) (Vila et al. 1997, Parker et al. 2004). Since, according to these authors, the wild species coyote (*C. latrans*) and wolf (*C. lupus*) diverged about one million years ago it is likely that the first dogs originated as early as 100 000 years before the present. Archaeological evidence suggests that during the late Pleistocene, humans and tamed wolves may have coexisted and that the change around 14 000 years ago from nomadic hunter-gatherer societies to sedentary agricultural populations resulted, owing to new

selective pressures, in marked phenotypic changes of the tamed wolves so that domestic dogs evolved. These results show that Darwin's speculations were wrong and that the "Bell-Lyell hypothesis" concerning the monophyletic origin of domestic dogs is supported by a large body of empirical evidence.

3 Animal domestication as an evolutionary process

In contrast to Darwin (1858, 1859, 1868, 1872a), Wallace (1858, 1889) argued that domesticated animals are no "model systems" for the elucidation of evolutionary processes that occur under natural conditions. In his "Ternate essay", he wrote that "no interference as to varieties in a state of nature can be deduced from the observation of those occurring among domestic animals. … Domestic animals are abnormal, irregular, artificial; they are subject to varieties which never occur and never can occur in a state of nature: their very existence depends altogether on human care" (Wallace 1858, p. 61). In his monograph entitled *Darwinism*, Wallace (1889) repeated his arguments against Darwin's assumption that artificial selection, i.e., the traditional breeder's approach, may be viewed as analogous to processes that occur in wild populations of animals and plants under the action of the selective forces of nature.

Can artificial selection be interpreted as "human-directed evolution", as suggested by Darwin (1858, 1859, 1868, 1872a) or were the arguments of Wallace (1858, 1889) correct?

Decades of research led to the conclusion that artificial selection is in fact nothing else than "human-directed evolution", as suggested by Darwin. Conner (2003) summarized the evidence for this interpretation of animal- and plant-breeding experiments and distinguished between two approaches. In the conventional version of artificial selection, a phenotypic trait of interest is measured in a sub-population of domesticated organisms, and the individuals with the most extreme phenotypic features are bred to produce the next generation. This experiment can answer the question of how rapidly a trait will evolve under a defined strength of selection. The second approach has been called "controlled natural selection" (Conner 2003), a strategy also known as "natural selection in a controlled environment". Here, the experimenter does not decide which individuals survive and reproduce, as is done in artificial selection, but rather imposes a defined environmental treatment, such as a temperature- or light regime, and lets the animals reproduce in this environment for several generations.

Many examples for rapid human-induced evolution under defined conditions are described in the literature on animal- and plant breeding research (Endler 1986, Bell 1997). One striking case study, the marked change in skull morphology of a purebred race of the domestic dog (*Canis familiaris*), is depicted in Fig. 3. The modern bullterrier shown in Fig. 3 A has a typical skull morphology that distinguishes this dog breed from most other domesticated varieties of the species

C. familiaris. A series of representative skulls of purebred bullterriers, collected between 1931 and 1976, a time interval which corresponds to only about 20 *C. familiaris*-generations, documents a rapid and gradual change in key anatomical features (Fig. 3). Moreover, the authors of this study (Fondon and Garner 2004) provided evidence for the molecular basis of this sustained evolutionary process. An analysis of the Runx-2 DNA-repeats (runt-related transcription factor 2-genes) in tissue samples of the 1931 bullterrier revealed a more intermediate allele (Q_{19} A_{14}) than was found in modern bullterriers (Q_{19} A_{13}).

In summary, this genetic analysis led to the general conclusion that frequent heritable length mutations in gene-associated, non-coding tandem repeats can generate large morphological variation on which breeders artificial selection can act. Moreover, the morphological data summarized in Fig. 3b indicate that there exists a continuum between micro- and macroevolution in mammals, as proposed by the "expanded synthetic theory of biological evolution" (Junker and Hoßfeld 2001, Carroll 2001, Simons 2002, Gould 2002, Kutschera and Niklas 2004, Kutschera 2005, Mayr 1963, 2001, Levit et al. 2004). However, as pointed out by Fondon and Garner (2004), the question of how widely this molecular mode of evolutionary change documented here in small, closed gene pools of domestic dogs is established in natural populations remains to be answered.

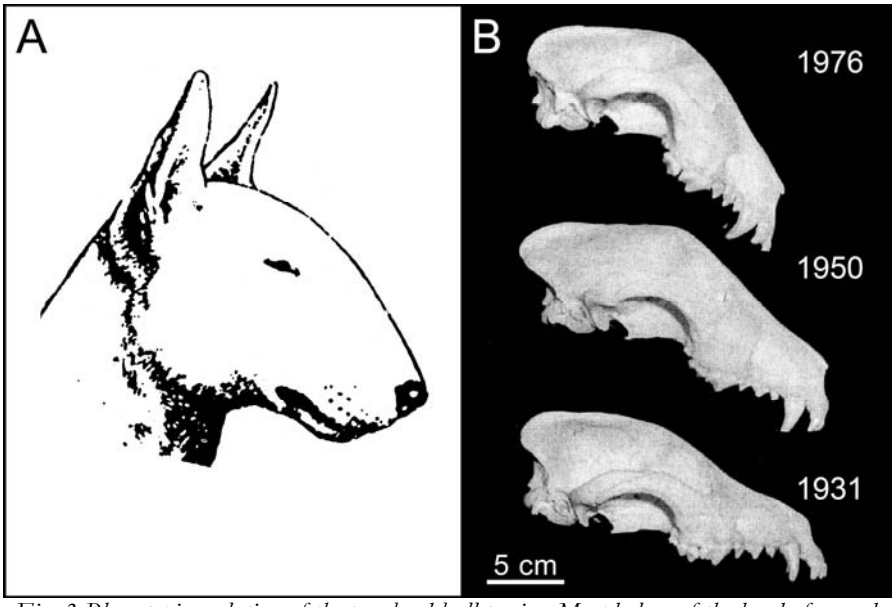

Fig. 3 Phenotypic evolution of the purebred bull terrier. Morphology of the head of a modern individual of this dog breed (ca. 1990) (A) and skulls from 1931, 1950 and 1976 (B). It is apparent that the characteristic facial features of this race evolved gradually over subsequent generations of artificial selection (adapted from Fondon and Garner 2004).

4 Charles Darwin, Herbert Spencer and the German shepherd dog breed

In one of his lesser-known books entitled *The Expression of the Emotion in Man and Animals*, Darwin (1872b) refers to Herbert Spencer (1820–1903), who coined the phrase "survival of the fittest" that was included by Darwin in later editions of his *Origin of Species* (compare Darwin 1859 vs. 1872a). In several of his writings, Spencer had described and analyzed the feelings of man. His concepts and interpretations are quoted in the "Introduction" of Darwin's (1872b) account. With respect to the belief in supernatural creations of animals and plants, he pointed out that "All the authors who have written on Expression, with the exception of Mr. Spencer –the great expounder of the principle of Evolution– appear to have been firmly convinced that species, man of course included, came into existence in their present condition" (Darwin 1872b, p. 10). After referring to the flight of certain breeds of the pigeon (Fig. 2) and the books of Spencer, Darwin (1872b) described three general principles of expression, which he illustrated by the description of "the lower animals", such as dogs and cats, as follows: "When a dog approaches a strange dog or man in a savage or hostile frame of mind he walks upright and very stiff; his head is slightly raised, or not much lowered; the tail is held erect and quite rigid; the hairs bristle, especially along the neck and back; the pricked ears are directed forwards, and the eyes have a fixed stare: These actions … follow from the dog's intention to attack its enemy" (Darwin 1872b, p. 50–51). To illustrate this behaviour, Darwin depicted a half-bred shepherd dog, which is shown in two states (Fig. 4 A, B). After a detailed description of two "carnivourous lower animals" (i.e., dogs and cats), he speculated that "In these cases of the dog and cat, there is every reason to believe that the gesture both of hostility and affection are innate or inherited; for they are almost identically the same in the different races of the species, and in all the individuals of the same race, both young and old" (Darwin 1872b, p. 57). This remarkable general conclusion has been corroborated by subsequent studies of the behaviour of dogs and cats. Darwin (1872b) interpreted his observations on domestic mammals in the light of evolution, and he was right.

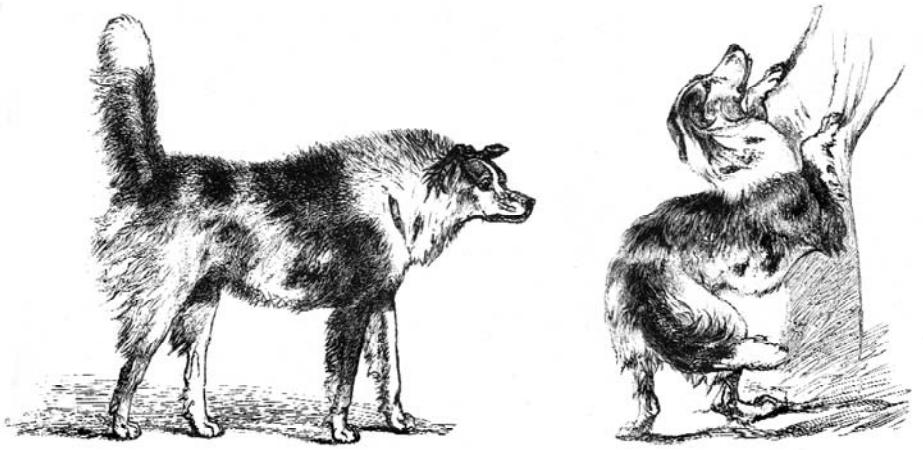

Fig. 5 Drawing of a half-bred shepherd dog that approaches another dog with hostile intentions (A) and the same individual caressing his master (B) (adapted from Darwin 1872b).

5 Origin and history of the German Shepherd dog

Fig. 4 Max von Stephanitz (1864–1936) was an ex-cavalry captain and former student of the Berlin Veterinary College. In April 1899, he founded the Society of the German Shepherd Dog. Photograph of the first German Shepherd, Horand von Grafrath. This male individual is recorded as the founding father of a breed, known as German Shepherd dogs.

During the 19th century, a variety of sheep dogs with phenotypes similar to the British individual depicted in Fig. 4 were widely known throughout Germany for their unique physical and mental qualities (i.e. strength), obedience and intelligence. In 1899, Captain Max von Stephanitz (1864–1936) (Fig. 5) purchased an individual,

named "Hektor Linksrhein", which represented to him the ideal combination of features necessary for intelligent, loyal working dogs. "Hektor", which was re-named by von Stephanitz "Horand von Grafrath" (Fig. 5), was the product of several generations of selective breeding and was therefore declared to be the first true German Shepherd. As a result, in April 1899 "Horand von Grafrath's" owner founded the "Verein Deutscher Schäferhunde, SV (Society for the German Shepherd Dog) and the male individual opened the society's inofficial register. In Volume 1 of the official German Shepherd breeding register ("Körbuch für Deutsche Schäferhunde") (Fig. 6), published in 1922, "Horand" is listed and depicted as the male founding father of this new breed of dog and his owner, von Stephanitz, wrote a long "Preface".

Immediately after the foundation of the "SV", "Horand" was bred with Shepherd dogs of desirable traits that were owned by other members of the society. Despite the fact that "Horand" fathered many pups, his most fertile "son" was "Hektor von Schwaben". As documented by the breeding register (KBDS 1922) (Fig. 6), "son Hektor" was another of his father's offspring to produce the unusually fertile male "Beowulf", who, throughout his life, fathered a total of 84 surviving puppies. Most of them were produced through deliberate inbreeding with "Hektor's" other offspring. Likewise, "Beowulf's" progeny were inbred and this population of genetically related Shepherds represents the stock from which all German Shepherds originate. A comparison of the first breeding register of 1922 (Fig. 6) with that published eight decades later (2002) may yield quantitative data (body size and -mass, etc.) on the lines of descent of the two distinct branches of the modern German Shepherd bloodline, the ideal show- and the robust working dogs. Such a detailed comparative analysis (KBDS 1922, Fig. 6 vs. KBDS 2002) is beyond the scope of this historical account of dog breeding, which was written with reference to Darwin's concepts and contributions on this topic.

Finally, it should be noted that, since ca. 1930, the German Shepherd became not only one of the world's most popular companion dogs, but also one of the most widely employed breeds for use as a "workhorse" for man. The tasks of the extant progeny of "Horand" (Fig. 6) include police work, jobs in the military and scent-work roles (narcotics- and explosive detection, cadaver searching etc.). From an evolutionary perspective it is remarkable that such a small inbreeding founder population (ca. 6 breeding lines, i.e. one founding "father" and several "mothers") gave rise to a dog breed with an average life span of 11 to 12 years that displays features such as intelligence, fearlessness, obedience, mental health and physical strength. It should be noted that effective population sizes of only about 10 adult individuals have been reported for some rare freshwater invertebrates in isolated habitats (Elliott 2008). However, some dog breeds provide good examples for non-beneficial breeding results. For instance, many so-called pedigree breeds have serious anatomical and physiological deficiencies, such as progressive retina atrophy which is common in English Mastiff dogs (Kijas et al. 2002). With reference to the case study of Fondon and Garner (2004) summarized above we

want to point out that the molecular basis of the German Shepherd dog breeding program, that originated with the concept and work of Captain Max von Stephanitz (Fig. 5), is largely unknown and therefore under investigation in our laboratory.


Körbuch
für deutſche Schäferhunde
1. Band
Ankörung 1922
Herausgegeben im Auftrage des Zuchtausſchuſſes des
„Vereins für deutſche Schäferhunde (SV)“,
Rechtsſitz München, EV im Kartell und PVZ
vom Zuchtbuchamt des SV, Abteilung für Körweſen
1922
Druck von Ant. Kämpfe, Jena

Fig. 6 Title page of Volume 1 of the breeding register published in 1922 by the Society of the German Shepherd Dog. Horand von Grafrath (Fig. 5) was the first mammal added to this ongoing list of dogs selected for breeding (courtesy of the Verein Deutscher Schäferhunde, München).

6 Conclusions

Animal domestication can be interpreted as human subjugation of wild mammals. It is commonly suggested that Stone Age hunters and gatherers started to isolate individuals of a suitable species from free-living populations and then selectively bred them to exaggerate desirable traits and eliminate unfavourable ones in a process known as artificial selection. Darwin (1858, 1859, 1868, 1872a) interpreted domestic animals as examples of artificial selection by man, analogous to natural selection in the wild. Wallace (1858, 1889), on the other hand, did not accept this conclusion and regarded domestic mammals as artefacts created by man. Several lines of evidence indicate that Darwin's view, which was to a large extent based on his extensive studies of domestic pigeons (Fig. 2), was correct, i.e., animal domestication is in fact an evolutionary process that may even be reversible

(Conner 2003, Fondon and Garner 2004, Daniel 2008). However, Darwin's conclusions as to the origin of the domestic dog were wrong and Lyell's hypothesis, which was based on Bell's observations, was right: the grey wolf is the ancestor of all domestic dog breeds known today. In response to the selection pressure of a new ecological niche, i.e., a domestic association with humans, wolves gradually evolved into dogs. We conclude that a detailed analysis of the breeding records, which contain data on body size etc. (Körbücher, Fig. 6) of one popular dog breed –the German Shepherd– may yield insights into the dynamics of this ongoing evolutionary process. Our first look into these detailed records was promising, but the exact kinetics of changes in body mass etc. over the course of 80 years of dog breeding are not yet known.

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References

Bell, G. (1997) Selection. The Mechanism of Evolution. Chapman & Hall, New York.

Bell, T. (1837) A History of British Quadrupeds, including the Cetacea. John van Voorst, Paternoster Row, London.

Carroll, S. B. (2001) Chance and necessity: the evolution of morphological complexity and diversity. Nature 409, pp. 1102 – 1109.

Conner, J. K. (2003) Artificial selection: a powerful tool for ecologists. Ecology 84, pp. 1650–1660.

DaCoPro (2008) Darwin Correspondence Project, Letter 2540a. www.darwinproject.ac.uk/darwinletters/calendar/entry–2540a.html

Daniel, S. O. L. (2008) Artificial selection, naturalization, and fitness: Darwin's pigeons revisited. Biol. J. Linn. Soc. 93, pp. 657–665.

Darwin, C. (1858) On the tendency of species to form varieties, and on the perpetuation of varieties and species of natural means of selection. I. Extract from an unpublished work on species, II. Abstract of a letter of C. Darwin, Esq., to Prof. Asa Gray. J. Proc. Linn. Soc. London 3, pp. 45–53.

Darwin, C. (1859) On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. John Murray, London.

Darwin, C. (1868) The Variation of Animals and Plants under Domestication. 2 Vols. John Murray, London.

Darwin, C. (1872a) The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. 6th ed. John Murray, London.

Darwin, C. (1872b) The Expression of the Emotions in Man and Animals. John Murray, London.

Elliott, J. M. (2008) Population size, weight distribution and food in a persistent population of the rare medicinal leech, *Hirudo medicinalis*. Freshwater Biol. 53, pp. 1502–1512.

Endler, J. A. (1986) Natural Selection in the Wild. Princeton University Press, Princeton.

Fondon, J. W., Garner, H. R. (2004) Molecular origins of rapid and continuous morphological evolution. Proc. Natl. Acad. Sci. USA 101, pp. 18058–18063.

Gould, S. J. (2002) The Structure of Evolutionary Theory. Harvard University Press, Harvard.

Junker, T., Hoßfeld, U. (2001) Die Entdeckung der Evolution. Eine revolutionäre Theorie und ihre Geschichte. Wissenschaftliche Bundesgesellschaft, Darmstadt.

KBdS (1922) Körbuch für deutsche Schäferhunde. 1. Band: Ankörung 1922. Druck von Ant. Kämpfe, Jena.

KBdS (2002) Körbuch für deutsche Schäferhunde. Band 2002: Ankörung 2002. Druck von J. P. Himmer GmbH, Augsburg.

Kijas, J. W., Cideciyan, A. V., Aleman, T. S., Pianta M. J., Pearce-Kelling, S. E., Miller, B. J., Jacobson, S. G., Aguirre, G. D., Acland, G. M. (2002) Naturally occurring rhodopsin mutation in the dog causes retinal dysfunction and degeneration mimicking human dominant retinitis pigmentosa. Proc. Natl. Acad. Sci. USA 99, pp. 6328– 6333.

Kutschera, U. (2003) A comparative analysis of the Darwin-Wallace papers and the development of the concept of natural selection. Theory Biosci. 122, pp. 343 – 359.

Kutschera, U. (2005) Predator-driven macroevolution in flyingfishes inferred from behavioural studies: historical controversies and a hypothesis. Ann. Hist. Phil. Biol. 10, pp. 59–77.

Kutschera, U. (2008) Darwin-Wallace principle of natural selection. Nature 453, p. 27.

Kutschera, U., Niklas, K. J. (2004) The modern theory of biological evolution: an expanded synthesis. Naturwissenschaften 91, pp. 255 – 276.

Levit, G. S., Hoßfeld, U., Olsson, L. (2004) The integration of Darwinism and evolutionary morphology: Alexej Nikajevich Sewertzoff (1866 – 1936) and the developmental basis of evolutionary change. J. Exp. Zool. (Mol. Dev. Evol.) 302 B, pp. 343 – 354.

Lyell, C. (1830–1833) Principles of Geology, being an Attempt to Explain the Former Changes of the Earth's Surfaces, By Reference to Causes now in Operation. Vols. 1–3. John Murray, London.

Mayr, E. (1963) Animal Species and Evolution. Harvard University Press, Cambridge.

Mayr, E. (2001) What Evolution is. Basic Books, New York.

Parker, H. G., Kim, L. V., Sutter, N. B., Carlson, S., Lorentzen, T. D., Malek, T. B., Johnson, G. S., DeFrance, H. B., Ostrander, E. A., Kruglyak, L. (2004) Genetic structure of the purebred domestic dog. Science 304, pp. 1160–1164.

Simons, A. M. (2002) The continuity of microevolution and macroevolution. J. Evol. Biol. 15, pp. 688 – 701.

Smith, C. H., Beccaloni, G. (Eds.) (2008) Natural Selection and Beyond: The Intellectual Legacy of Alfred Russel Wallace. Oxford University Press, Oxford.

Vila, C., Savolainen, P., Maldonado, J. E., Amorin, I. R., Rice, J. E., Honeycutt, R. L., Crandall, K. A., Lundeberg, J., Wayne, R. K. (1997) Multiple and ancient origins of the domestic dog. Science 276, pp. 1687–1689.

Wallace, A. R. (1858) On the tendency of species to form varieties, and on the perpetuation of varieties and species of natural means of selection. III. On the tendency of varieties to depart indefinitely from the original type. J. Proc. Linn. Soc. London 3, pp. 53–62.

Wallace, A. R. (1889) Darwinism. An Exposition of the Theory of Natural Selection with some of its Applications. MacMillan&Co., London and New York.

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