THE USE OF CONVERGENCE AS A TOOL IN THE RECONSTRUCTION OF HUMAN PAST, WITH SPECIAL FOCUS ON WATER USE IN HOMININ EVOLUTION

APPENDICES

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APPENDIX A – DISCREPANT ORGANISMS: PROBLEMS IN THE CLASSIFICATION OF ORGANISMS IN PRE-DARWINIAN TIMES

In this Appendix the focus is on the role of analogy in pre-Darwinian natural science. It will be argued that convergent organisms (in form of "epistemological discrepant organisms", see below) and analogical reasoning led to fruitful insights with enormous impact in 18th century natural history. As argued in Appendix B, this development resulted in the first extensive hypothesis on the evolution of organisms in that period.

A.1 Epistemological discrepant organisms: Definition

I proposed the term "epistemological discrepant organisms" (or simply "discrepant organisms")[1] to designate taxa or species difficult to place in a single logical category in pre-Darwinian zoological treatises due to their ambivalent anatomy or behaviour. Naturalists in pre-Darwinian times encountered important difficulties in understanding and distinguishing two kinds of similarities between living organisms. On the one hand, since several species share innumerable evident similarities, it was possible to infer intuitively that, for instance, mammals are closely related to each other. On the other hand, humans could not ignore that organisms could be also linked to each other by other criteria, such as the environment in which organisms live (e.g., reflected in the traditional division of aquatic, flying and terrestrial animals) or by stressing the functional similarity in certain features (e.g., the "wings" of insects, birds and bats). Puzzling to the same degree in pre-Darwinian times was the almost identical inner anatomy of animals living in completely different environments (e.g., dolphins and pigs), or the question as to why the inner anatomy of tuna fishes and dolphins is so radically different, although these organisms resemble each other strongly in their external anatomy and their ways of life. These different ways how to categorize organisms were not compatible to each other due to the absence of a sophisticated theory on the evolution of organisms. These epistemological discrepancies played a crucial role both in early static

[1] This expression was first used in a supplemental volume to an unpublished diploma thesis by the present author (Bender 1999b). In German, the expression "*epistemologische Dissonanz*" has an apparent similarity to the term "cognitive dissonance" used in psychology (Festinger et al. 1956). Both terms share some similar ideas but are not identic. Leon Festinger and colleagues used the term "cognitive dissonance" to describe the discomfort experienced by people when simultaneously holding two or more conflicting cognitions. The expression "epistemological discrepant organisms", on the other hand, refers to the specific problems caused by convergent organisms (whole taxa or single species) in early attempts to build up a coherent system to classify organisms. In retrospect (I did not know Festinger's concept in the 1990's), I think that the issues related to epistemological discrepant organisms can be regarded as a specific case of cognitive dissonance, in which problems produced by conflicting information are widely ignored. In a recently published work, the expression "incidents" (German *Störfälle*) was used in a very similar sense as epistemological discrepant organisms (Bühler 2011).

hierarchic views of nature (*scala naturae*) and in the first attempts to formulate a scientific evolutionary hypothesis in 18th century (see Appendix B).

A.2 The polarity induced by discrepant organisms

Generally, discrepant organisms were perceived as paradoxical because they exhibit features atypical for closely related species; rather, they were perceived as functionally related to distantly related creatures (see Table A.1). The polarity induced by discrepant organisms is an important factor to understand pre-Darwinian efforts to categorize organisms. If a naturalist grouped organisms by focusing on aspects of functionality or life-form, as in the example above on dolphins and tuna, a closer investigation of affinities between the organisms tended to split them, often lumping together organisms with strong divergent life-forms or body shape. There are uncountable examples for these conflicting perspectives. In zoological treatises of the Middle Age bats were often described together with birds (see references in Wegmann 2005). Since the expression "flying creatures" (analogous to the terms "aquatic creatures" and "terrestrial creatures") was a common one both in colloquial and scientific language, naturalists in pre-Darwinian times explicitly had to point out the divergent affinity between distantly related flying organisms. For instance, in a popular book on science first published in 1670, the author investigated the question: "Are the bats birds or not?" (*Sind die Fleder-Mäuse Vögel oder nicht?*) (Voigt 1980, 56). The author reasoned that besides the fundamental anatomical divergencies between bats and birds, the ability to fly can be found in other organisms like insects and even some fishes, and he went on to ask the question "Who wants to categorise them as birds?" (*Wer will sie aber mit unter die Vögel rechnen?*) (Voigt 1980, 57). A similar reasoning is implied in a statement by the Swiss naturalist Conrad Gesner (1516-1565). In a booklet published in 1541 – probably the first comprehensive review of milk and milk products – he explained that among the birds only the bat produces milk (Gesner 1996, 89).

A further example is related to the discovery of the monotreme platypus. This semi-aquatic, egg-laying mammal with its webbed feet and a "beak like a duck" was first categorized as a hoax at the end of the 18th century, when a dried specimen initially reached England (Moyal 2001). In this case, the perceived anomaly was generated not only through convergent similarities between ducks and the platypus, but also through the distinction between viviparous and oviparous animals, which was radically challenged by the new species. For these reasons, platypus and other monotremes were regularly classified as intermediary forms. For instance, Johann Wagler (1830) classified platypus along with other aquatic vertebrates

(including the flying reptile *Pterodactylus*, which was sometimes regarded as aquatic; see Fig. A.1 below) in the bizarre class Gryphi (in German *Greife*). He described them as organisms with the combined features of mammals, birds, reptiles, and fishes (Wagler 1830, e.g., 66).

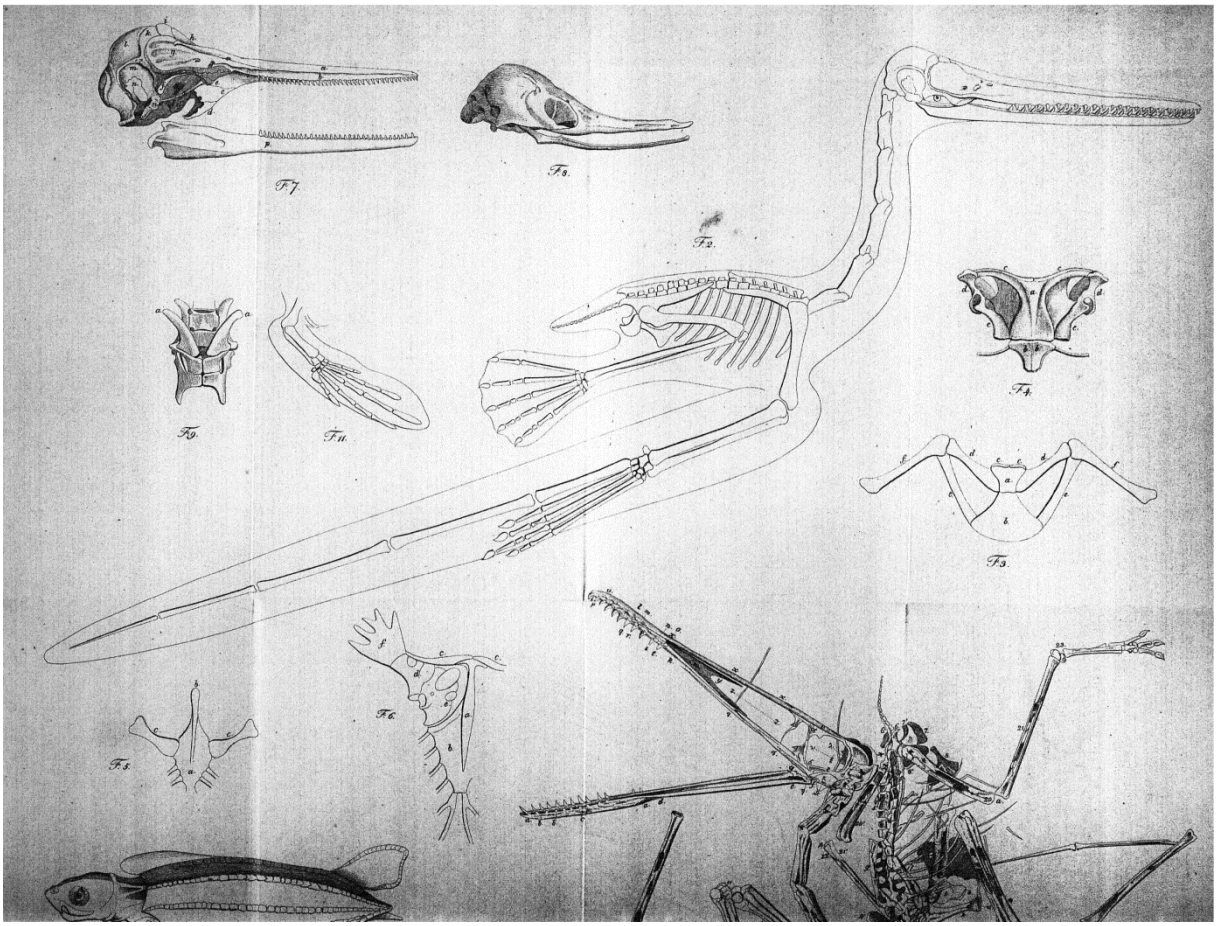


Figure A.1: Gryphi as a bizarre taxon in pre-Darwinian zoology. Wagler's reconstruction of *Pterodactylus* as an aquatic animal as depicted in his book *Natürliches System der Amphibien* (1830)

Table A.1 Examples of epistemological discrepancies (for references see text)

General perception of characteristic features of certain organisms in opposition to other taxa	Discrepant organisms …	… and the specific source of epistemological discrepancies
In opposition to mammals, **birds** are able to fly and do not exceed a certain body size	Ostriches…	… do not fly and exceed the body size of other birds
In opposition to fishes, **mammals** are terrestrial	Several aquatic mammals…	… are exclusively aquatic and have an external appearance of fishes
In opposition to birds, **mammals** are quadruped and are not able to fly	Bats…	… have wings and are able to fly
In opposition to mammals, **fishes** lay eggs	Most sharks…	… are ovoviviparous, and like most mammals, give birth to fully alive and functional young
In opposition to birds, **mammals** do not have a beak and do not lay eggs	Platypus…	… has a beak-like organ and lay eggs
In opposition to plants, **animals** are mobile	Sea anemones and corals (Anthozoa)…	… live attached to a substrate and resemble flowers (Anthozoa: "flower animals"); see discussion and references in Bühler (2011)
In opposition to animals, **plants** do not hunt and consume animals	Carnivorous plants…	… trap and consume animals
In opposition to non-mammals, **mammals** have a fur to protect them against the cold and are quadrupeds	Humans…	… do not have a thermoregulatory efficient fur and are bipedal
	Cetaceans…	… do not have a thermoregulatory efficient fur; their forelimbs are modified into flippers and they hindlimbs are vestigial and externally not visible
In opposition to birds, **fishes** do not have wings and are not able to fly	Flying fishes…	… have wings and are able to "fly"
In opposition to terrestrial animals, **fishes** live in water and are not able climb	Climbing fishes…	… like the climbing gouramies (Anabantidae) are able to breathe atmospheric oxygen and "climb" out of water
In opposition to "worms", **vertebrates** have legs	Snakes, eels and blindworms…	… do not have legs

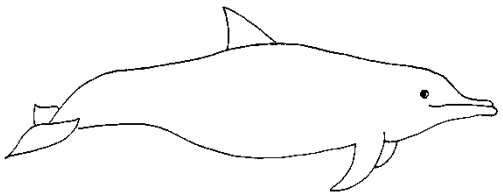
A.3 The role of secondary aquatic organisms

Secondary aquatic animals were among the greatest challenges in pre-Darwinian zoology.[2] Aristotle (384 BC-322 BC) was the first naturalist to explicitly recognize that the cetaceans are distantly related to fishes (see Bäumer 1988), giving very specific reasons for the

[2] For a review of the scientific journey of cetaceans from fish to mammals in the history of science see Romero (2012); I found this excellent historical investigation only few days before the final submission deadline of the present thesis, so that the review could not be considered here.

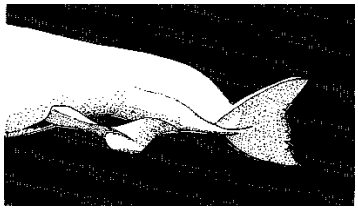
differentiation: (a) dolphins have bones, and not fish-spines[3]; (b) they do not have gills[4] but lungs[5]; when caught in a net, a dolphin quickly suffocates for lack of air[6]; (c) dolphins and whales breastfeed their young[7] and (d) are live-bearing[8]. Although he established that terrestrial mammals breathe air and are live-bearing organisms, he was seemingly confused by the fact that some animals did not fit into a simple classificatory schema (see Fig. A.2), as evident in following sentence: "For it is not easy to class each of these either as solely water animal or as land animal, if one is to class those that take in air as land animals and those that take in water as water animals by nature". [9] The "fish-like" dolphins, for instance, were an exception under most aquatic vertebrates, since they had the physiology and inner anatomy of terrestrial mammals. On the other hand, several "live-bearing" sharks seemed to be an exception to most aquatic vertebrates, which usually lay eggs.

[3] (Hist. anim. III 7, 516 b 12).
[4] (Hist. anim. I 5, 489 b 3; Hist. anim. VI 12, 566 b 3).
[5] (Hist. anim. II 15, 506 b 1-3; Hist. anim. VI 12, 566 b 14-15).
[6] (Hist. anim. VIII 1 589 b 7-8).
[7] (Hist. anim. II 13, 504 b 21; Hist. anim. III 29, 521 b 23-24).
[8] (Hist. anim. I 5, 489 a 35-b 2; Hist. anim. II 13, 504 b 21-22; Hist. anim. VI 12, 566b 2).
[9] (Hist. anim. VIII 2, 589 b 7-9).



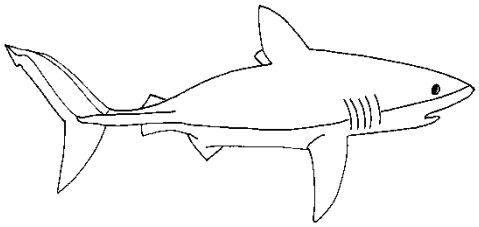
(a)

„fishlike“ dolphins with features of ➔



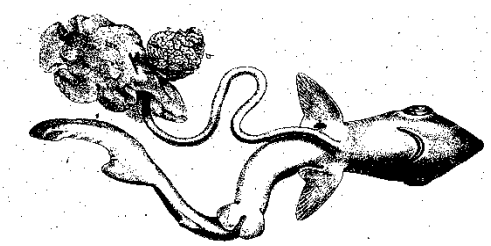
(b)

live-bearing, air breathing mammals (mostly land animals)



(c)

„live-bearing“ sharks with features of ➔



(d)

in water breathing organisms with a fish form (mostly egg laying water animals)

Figure A.2: Examples of problems in Aristotelian zoology caused by epistemological discrepancies. (b) after a photo of a bottle-nose dolphin (*Tursiops*) by D. K. Caldwell (in Bateson 1988); (d) from Müller (1842); (a) and (c) from Bender and Oser (1997).

It is interesting to see what Aristotle understood by "analogy" [ἀνάλογον][10]: "[S]ome animals have a lung, others have no lung but something else to correspond instead of it, again, some animals have blood, while others have its counterpart, which in them has the same value as blood in the former" (De part. anim. I 5, 645 b 6-10). From this sentence is evident that Aristotle used the term "analogy" to characterize non-homologous features which share a similar function. Yet another passage of the same work shows that he was not able to discern clearly between similarities in the sense of convergences and similarities in the sense of homology. He argued that while one bird differs from another bird by variation of the same features (e.g., one has longer, the other has shorter feathers), the difference between a bird and a fish is more substantial, "and their correspondence is only by analogy: a fish has no feathers

[10] The use of the concept of analogy by Aristotle was investigated by other authors (Fiedler 1978; Lloyd 1971). Another important aspect in ancient classification of living beings is the principle of "same to same" (in German: *Gleiches zu Gleichem*), as investigated by Müller (1965).

at all, but scales, which correspond to them" (De part. anim. I 4, 644 a 21). Problems in Aristotelian zoology caused by the apparent anomaly raised by dolphins and whales (see Balmer in Aristotle 1993, 66-69) are related to the notion that his biological views were developed without any concept of species mutability (Cole 1944, 36; Mayr 1982, 305-307).

The problems caused by discrepant organisms in the classification of aquatic mammals had a longstanding effect on the work of pre-Darwinian naturalists. For instance, in his book *De aquatilibus* (1553), the French physician and botanist Pierre Belon (1517-1564) denominated the cetaceans as *pisces,* even after he recognized that the inner organs of a dolphin are similar to those of a *porci terrestris* (terrestrial pig) (Belon 1553, 12). In his anatomical description of dolphins, the London physician Edward Tyson (1651-1708) was astonished by the discrepancy between the external similarity between dolphins and fishes and their inner "pig-anatomy" (Tyson 1680, 26). A similar astonishment was expressed by the French missionary and traveller Jean de Léry (1534-1613). In his *Histoire d'un voyage fait en la terre du Brésil* he pointed out that a slashed dolphin had a curious similarity with an "ordinary terrestrial pig" (*un naturel porc terrestre*) (De Léry 1972, 49 (first ed. 1578)). In the 16th century the Caribbean manatee (*Trichechus manatus*) was occasionally described as a fish and a terrestrial animal as well (e.g., Garcia et al. 1973, 257), obviously pointing to its mammalian nature with the term "terrestrial", as most mammals are terrestrial. In a very influential book first published 1692, the druggist Pierre Pomet used frequently the term "fish" undifferentiated to describe fishes, crabs and aquatic mammals, as for instance a manatee (pp. 591-596), cetaceans (pp. 579-584) and seal (pp. 603-604) (Pomet 1987).

As an aside it should be mentioned that although the convergence in body shape between cetaceans and fishes played an important role in the early denomination of "fishes" for several aquatic mammals, this umbrella term was not exclusively the product of an early misinterpretation of zoological diversity. To a certain degree, the misinterpretation was also purposefully created, as in the case of the "fish-nature" of birds, a concept defended until the 18th century. With the inclusion of rigid fasting rules in the Christian tradition in the Middle Ages, lay people were not allowed to eat meat on fast days, with the exception of fish. Since these rules had a permanent character in some monasteries and convents, some scholars tried to circumvent them through a free interpretation of the Genesis. This led to a "culinary

advantageous" but zoologically absurd classification of organisms in which birds[11] and other animals became closely related to fishes.

A.4 Discrepant organisms as "bridges" in *scala naturae*

Organisms were often depicted in *scala naturae*, an ancient concept which became very popular in the 18th century and was used to establish a hierarchic organization of inanimate and animate objects in a continuous and mostly static scale of perfection (Anderson 1976; Appel 1980; Fabian 1964; Lovejoy 1936; Thienemann 1909). It is interesting to see how discrepant organisms were often used as "bridges" between distantly related taxa (see Figure A.4). Aristotle, among others, saw (a) the bats as intermediary between birds and quadrupeds[12], (b) the seal as a link between quadrupeds and fishes[13], (c) the ape as an intermediate form between man and quadrupeds[14]; additionally, (d) he also mentioned bats and ostriches as organisms sharing features from different groups[15]. The Aristotelian tradition of listing discrepant organisms as intermediary forms was maintained in the 18th and 19th centuries, for example, in early evolutionary ideas (see below), in naive zoology expressed in religious (Martinet 1780, 10) or mystical works (Schubert 1808, 279, 207-208, 282), and in zoological works written in the Aristotelian tradition (Meyer 1855). Even after 1859, some authors felt encouraged to recycle uncritically elements of ancient zoological treatises. The German Orientalist Friedrich H. Dieterici, for instance, used his deep knowledge of ancient Arabic treatises in his attempt to criticize and replace Darwin's ideas. Ignoring largely the zoological knowledge available in his time and inspired by superficial analogies among organisms organized in an all-embracing *scala naturae*, he formulated erroneous ideas of distantly related organisms [as] evolving from each other.[16] Another example of naive evolutionary ideas in which convergent organisms were envisaged as closely related is

[11] Interesting in this context is the myth in which the barnacle goose (*Branta leucopsis*) was depicted as growing inside shells hanging down by their beaks on trees, falling after a certain time in water, where they could complete the transition to adult animals (Krause 1880, 181-182; Riedl-Dorn 1989, 89-99). For an early text on this topic see Sorel (1637, vol. 1, 330-331); as we will see in Appendix B, Sorel was an important author for de Maillet's evolutionary and pluralistic views. A similar medieval story of vertebrate developing ontogenetically from a completely unrelated taxon concerns the fable of the zoophyte Tartar lamb, which described a sheep springing from the seeds of a fruit (Appleby 1997; Lee 1887). Both myths were probably motivated by naive analogical connections between parts of plants and animal features (in the case of the Tartar lamb: an analogy between cotton and sheep wool).

[12] (De part. anim. IV 13, 697 b 8-11).

[13] (Hist. anim. II 1, 501 a 20-25; De part. anim. IV 13, 697 b 8-11).

[14] (Hist. anim. II 8, 502 a 16-18).

[15] (De part. anim. IV 14, 697 b 15-24).

[16] He believed for instance that camels descended from giraffes. Haunted by lions, a group of giraffes arrived in an arid region covered by undergrowth and brushwood. There they were forced to eat at the ground, and so their neck became bent and a hump was formed (Dieterici 1878, 59-62).

supplied by Gustav Steinmann's statements on dolphins evolving from *Ichthyiosaurus* (see Appendix D). See also the books by the German Edgar Dacqué, who was a respectable palaeontologist until he began to publish evolutionary ideas from a natural philosophical and religious perspective (Dacqué 1924; 1952).

Ancient thinkers and pre-Darwinian naturalists often were attracted by analogies between the development of an individual (ontogeny) and the evolutionary history of a lineage; this topic was reviewed by Stephen J. Gould (1977) and J. A. Kleinsorge (1900) and will not be repeated here. A yet ignored and remarkable example of speculations proposed by the German naturalist and natural philosopher Lorenz Oken (1779-1851) was published in the paper *Entstehung des ersten Menschen* (Descent of first humans) (Oken 1819). Beginning from an analogy between the amniotic fluid (in which the human foetus is immersed, see Fig. A.3) and a temperate primordial ocean, he described a surrealistic scenario of legions of babies, each floating encapsulated in an individual uterus in a primordial ocean, some arriving at a beach, coming out of the uterus and crawling onto the shore, eating shells or drinking the milk of goats and eventually surviving at the seaside.

Figure A.3 An aquatic baby as depicted in Oken's paper on the "descent of first humans" (Oken 1819)

Oken's vision evokes ideas expressed by Anaximander[17] and by De Maillet, but also anticipates some concepts later expressed by depth psychologists; see Bender (1999a, 84-85). Oken's natural philosophical speculations illustrate to what extent an early 19th century[18]

[17] Oken's ideas are very close to Anaximander's (see Appendix B). Although Oken replaced the spiny bark of Anaximander's scenario by an amniotic sac, his speculations on babies surviving by themselves after reaching the coast are basically the same as Anaximander's views.

[18] Similar bizarre ideas implying an analogy between a primordial ocean and the amniotic fluid can be found in the works of early (Steiner 1979, 20ff) and modern (König 1981, 9ff) anthroposophists and in the still popular concept promoted by depth psychologists; see explanations in Bender (1999a, 84-85). A remarkable example of radical natural philosophic ideas expressed by a trained zoologist can be found in the works by the German cryptozoologist François de Sarre (1992; 1994a; 1994b). He merged the concept of the aquatic hypothesis with elements of Max Westenhöfer's *Primitivitäts-Hypothese* and de Maillet's ideas on *hommes marins;* the result of

naturalist was ready to sacrifice rationality in attempt to describe uncritically visions based on naive analogies.

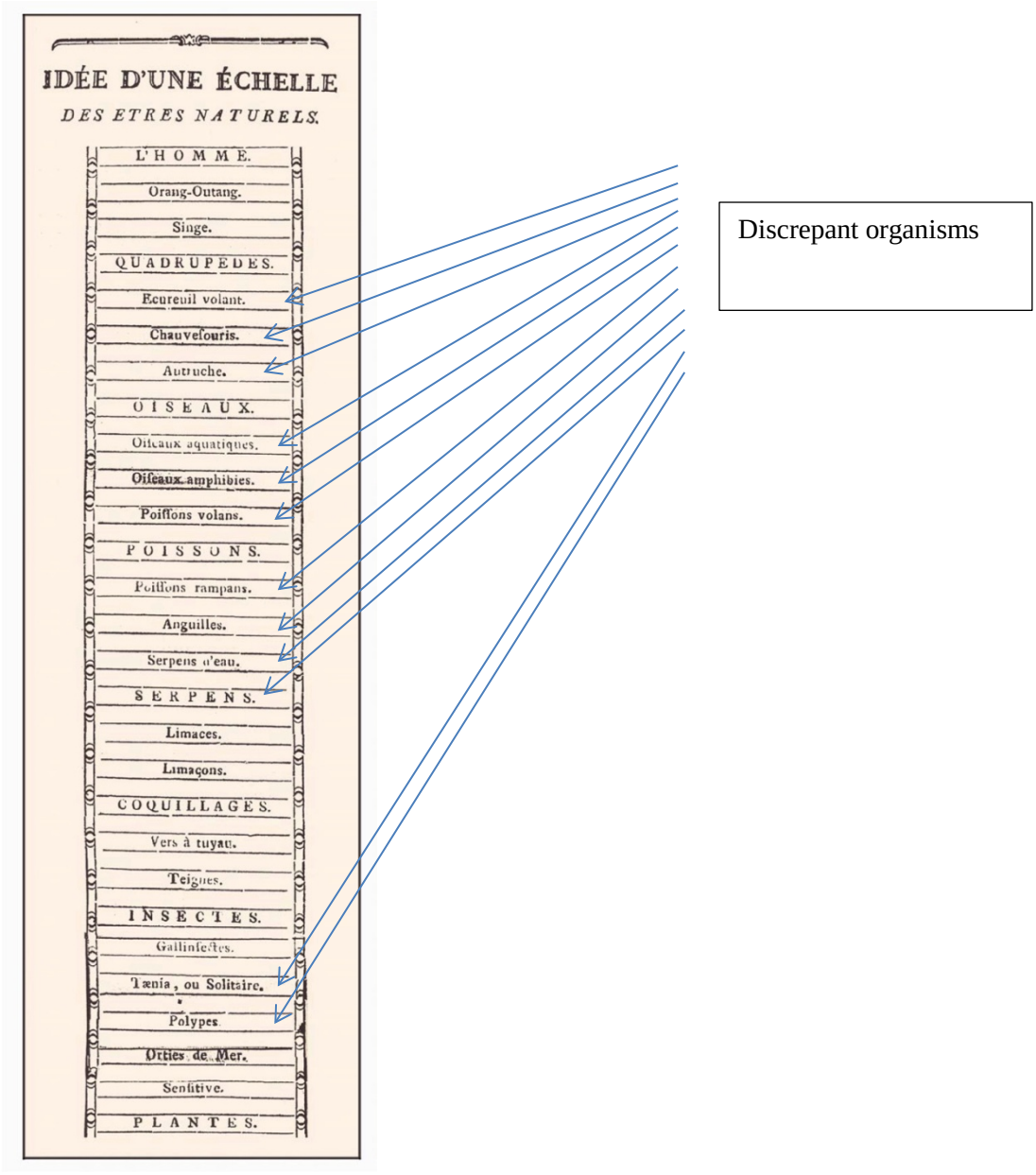


Figure A.4: The use of discrepant organisms in *scala naturae*. Charles Bonnet and other early naturalists frequently used discrepant organisms to bridge distantly related taxa within linear and hierarchical schemes in the Aristotelian chain of beings. In this case, the discrepant organisms are: flying squirrels, bats, ostriches, amphibian fishes, amphibian and aquatic birds, flying fishes, climbing fishes, eels, aquatic snakes, snakes, and polyps; from Bonnet's *Oevres d'histoire naturelle et de philosophie* (Bonnet 1779, vol. 1, xliv)

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this interesting eclecticism can be guessed from the title of one of his works, *Sirènes et hommes-marins : Du mythe à l'évidence scientifique* (Cazottes & de Sarre 2006).

It is interesting to see that Westenhöfer himself kept his *Aquatile Hypothese* rather disconnected from his main ideas, probably aware of the problems of merging incompatible concepts (see Appendix F).

The problems related to a linear (or multi-linear) *scala naturae* and the use of discrepant organisms to fill gaps between what is today recognized as distantly related taxa became evident with the definitive dissemination of evolutionary ideas in the decades following the publication of Charles Darwin's *Origin of Species* in 1859.

A typical analogy carried out by early naturalists was the comparison between plants and animals. For instance, the Greek Theophrastus (c. 371- c. 287 BC) wrote in his *Enquiry into Plants* that "we must not assume that in all respects there is complete correspondence between plants and animals" (Theophrastus 1916, 7), and continued:

> Again many plants shed their parts every year, even a stags shed their horns, birds which hibernate their feathers, four-footed beasts their hair: so that it is not strange that the parts of plants should not be permanent, especially as what thus occurs in animals and the shedding of leaves in plants are analogous processes. In like manner the parts concerned with reproduction are not permanent in plants; for even in animals there are things which are separated from the parent when the young is born, and there are other things which are cleansed away, as though neither of these belonged to the animal's essential nature. And so too it appears to be with the growth of plants; for of course growth leads up to reproduction as the completion of the process. (Theophrastus 1916, 7)

Naturalists had different ideas about the reason for such "analogies" between plants and animals. When discussing the topic in his *Horae Entomologicae or Essays on the Annulose Animals*, 1819-21, the Anglo-Australian naturalist William Sharp Macleay (1792-1865) used discrepant organisms as bridge between plants and animals:

> On the whole however it appears that animals are to be distinguished by the existence of an absorbent intestinal cavity, and of a nervous system, and that both these marks become indistinct in the infusoria and polypes[19]. It follows therefore that the infusoria and polypes, which are the most simple of all animals in structure, approach nearest to the vegetable nature. (Macleay 1821, 198)

[19] In the discussion of the analogy between plants and animals, early naturalists often refer to the zoophytes. The term was used by medieval and renaissance texts on the one hand to explain animals emerging developing ontogenetically from plants (see footnote 11 on Tartar lamb), or on the other hand to describe animals which superficially resembled plants, like a sea anemone (Actiniaria). Not all scholars in this time accepted this term. For instance, after listing the features which he considered unique to animals and plants (Lamarck 2006, 195-197), Lamarck rejected the term zoophyte by arguing that a class of animals should not receive a name "which embodies a false notion of the objects indicated" (Lamarck 2006, 200).

In pre-Darwinian times, bridging plants to animals did not necessarily imply evolutionary thoughts, but were often justified by the existence of a divine plan in nature. In his *An Inaugural Dissertation on the Analogy between Plants and Animals* (1806), William F. Selby wrote: "With what order and uniformity do the laws of nature exist, through the vast fabric of creation, every part thereof plainly demonstrating that we are all the offspring of the same parent" (Selby 1806, 24). Early naturalists had different ways to accommodate the difficulties caused by epistemological discrepancies. Macleay presented his own hypothesis on classification of organisms – the quinary or circular system.[20] In his view, organisms could not be classified in a linear, but rather in a flexible schema in which two kinds of organismic relationships - affinities and analogies – were taken into account. In pre-Darwinian times, affinity denoted a genealogic relationship and was therefore used in a similar way as the modern term homology.[21] However, because of the lack of a concept of relationship due to common ancestry, affinity referred to an abstract relationship between organisms, often implying an idealistic similarity between taxa. Analogies, on the other hand, as they were used by Macleay, consisted in a "correspondence between certain insulated parts of the organization of two animals which differ in their general structure" (Macleay 1821, 363). In this sense, it was similar to the concept of convergence. Macleay tried to link distantly related groups of organisms by referring to different degrees of perfection in discrepant species. He used among others the superficial similarity between fishes and cetaceans to illustrate his ideas:

> Be this however in general as it may, there is one thing very certain, that the Cetacea lead us by a very distinct and natural transition from the Mammalia to the Fishes; and that if their warm blood, their lungs, their viviparous generation and mammae prove their affinity to the former group, their skeleton and external covering, the imperfection of their olfactory and auditory organs, all show that they approach near to the fishes. (Macleay 1821, 272)

Following the same logic, Macleay tried to identify fishes having some traits approximating those of mammals. He believed he found them in the form of viviparous sharks, "with their ear more perfectly organized than that of other fishes, and their body destitute of scales, the

[20] Maclean's and other classifying systems in this time were investigated by different authors (Di Gregorio 1982; Endersby 2005; O'Hara 1991; Ritvo 1997; Winsor 1976).

[21] The plurality of terms concerning homology in pre-Darwinian discussion was aptly described by Stevens with following words: "In the early part of the nineteenth century there was a complex semantic web around words signifying relationships and resemblances - words such as 'primitive', 'type', 'essence', 'organization', 'symmetry', and 'analogy'. From this web emerged the term 'homology' [.]" (Stevens 1984, 78); see also Stevens (1994, 185-198) for the complex interconnections between pre-Darwinian concepts such as analogy, affinity, parallelism and design, especially in botany.

particular disposition of their fins, and their closed branchiae, all indicate at what place we are to enter among the fishes" (Macleay 1821, 272).

It ought to be expected that the lack of a clear distinction between closely related and functionally related organisms would have been a strong obstacle for an early naturalist to gain a first insight of living organisms as a product of an evolutionary process. However, as argued here, quite the opposite is true. Modern historians of science hold a popular belief that the first evolutionary ideas[22] arose through the awareness of great time dimensions offered by geological works. Although certainly true, the arguments put forward here are that some important concepts of great time dimensions defended in early geological works are the direct consequence of developments which took place in cosmological discussions; specifically through the increasing conviction that the universe was immense, which in turn instigated an intensive debate on the existence of extra-terrestrial life. This awareness was the direct product of the Copernican revolution. The link between the Copernican revolution and the origin of evolutionary ideas is evident in the views proposed by the French diplomat Benoît de Maillet, as follows in Appendix B.

[22] To avoid anachronism, historians of science have proposed several terms to replace the word „evolution" in discussions of pre-Darwinian ideas on the succession of life forms which strongly resemble the evolutionary process. In the present work, the term evolution is used in connection with several pre-Darwinian evolutionary concepts. This terminology does not imply any preconceived idea on similarities in arguments between pre-Darwinian and Darwinian concepts.

APPENDIX B – THE USE OF ANALOGIES WITHIN THE PLURALITY OF WORLDS-DISCUSSION LEADING TO AN EVOLUTIONARY SYSTEM

B.1 Introduction

Biological research in 18th and early 19th century experienced extraordinary developments. Starting in the period of "enlightenment" of science, which corresponds broadly on a temporal scale to the "rational infiltration" [*rationale Durchdringung*] in biology in the 17th century (Ziswiler 1982), the increasing impetus of biology was directly related to data supplied by (a) the voyages of discovery; (b) by the new methods of taxidermy (Belozerskaya 2006; Rácek 1990)); (c) by the invention of the microscope; and (d) by the inventories made by menageries and zoos (Baratay & Hardouin-Fugier 1998), botanic gardens, curiosity cabinets (Daston & Park 1998; Mauriès 2002), and later by museums (Alexander 1983). However, all these data gave rise to new problems. The specimens avidly collected had to be described, identified, and catalogued according to a certain system. Although the Linnaean classification, the most influential system since the publication of different editions of Linnaeus' *Systema Naturae* (first edition 1735) was certainly as an immense improvement in the establishment of taxonomy, it was – as well known – not based on an evolutionary concept and was rather arbitrary in certain aspects.[23] Furthermore, the number of organisms collected was immense, and the conditions in the storage areas of the leading museums were absolutely catastrophic - a situation diametrically opposed to the picture of a harmonic and orderly nature (Voss 2011). The book *Telliamed* written by the French diplomat and naturalist Benoît de Maillet (1656-1738) - first circulated as a manuscript and was printed in Amsterdam (De Maillet 1748) ten years after de Maillet's death – played a crucial role in the early attempts to interpret organismic diversity within a transformist framework.

However, historians have expressed very contradictory opinions on the importance of de Maillet's work. On the one hand, some early authors regarded it has essential in the history of evolutionary thinking and of geology[24]; on the other, there has been a long tradition in biology to classify de Maillet's ideas as a curious echo of Middle Age superstition in the 18th century, or to list different arguments in an attempt to demonstrate that the de Mailletian system lacked any evolutionary concept.[25] For this and other reasons, modern biological

[23] For example, concerning the invertebrates, the Linnaean system "was a backward step from that of Aristotle" (Mayr 1982, 182).
[24] See chapter B.4.3 on the positive evaluation of *Telliamed* by early authors.
[25] See chapter B.4.3 on the negative reception of *Telliamed*.

textbooks presenting an outline of the emergence and crystallization of evolutionary ideas usually ignore de Maillet's crucial contribution.[26]

After outlining de Maillet's biography and the content of *Telliamed*, this investigation will focus on three aspects of de Maillet's work which have not been fully appreciated. First, I will argue that the common evaluation of de Maillet's hypotheses on evolution (usually considered naive and an indication of his lack of biological knowledge and common sense) are misleading in several aspects. Most negative evaluations adopt uncritically biased views expressed or by *opponents* of evolutionary ideas in 18th and 19th century or by early authors with only superficial knowledge on de Maillet's work. Second, I will show that the interplay between de Maillet's hypotheses and cosmogenetic ideas is essential to understand the emergence of evolutionary thinking in the 18th century. In the present thesis I will suggest that de Maillet's evolutionary ideas were strongly influenced by the temporal and spatial expansion (and the intensive discussion on the plurality of worlds[27]) which followed the Copernican revolution. In other words, the first extensive evolutionary system is a specific attempt to interpret geological and biological phenomena within the cosmological perspectives supplied by the Copernican revolution. Finally, I will argue that the specific use of analogies in de Maillet's evolutionary ideas was crucial for the dissemination of the concept of species change. The importance of these analogies is well illustrated by their partial adoption by other early evolutionists, like Lamarck and Goethe. This historical background is essential to understand the emergence of Lamarck's hypothesis on primeval man as a creature evolving on open plains (see Appendix D), an idea still influential in modern palaeoanthropology.

B.2 Benoît de Maillet: his life and main work *Telliamed*

Biographic information on de Maillet is supplied by *Vie de M. de Maillet*, written by the publisher of *Telliamed*, Abbé Jean Baptiste le Mascrier. This text appeared in the last French edition of *Telliamed* (Le Mascrier in De Maillet 1755, vol. I, 9-33); further biographical information comes from de Maillet's correspondence (Benitez 1980; Rothschild 1964; Rothschild 1965; Rothschild 1968) and other sources.

De Maillet was born 1656 in Lorraine, and received an excellent classical education. According to Le Mascrier (in De Maillet 1755, vol. I, 10-11, 32-33), de Maillet was appointed

[26] See chapter B.4.2.

[27] The term "plurality of worlds" (in German *Weltenvielheit*, in French *pluralité des mondes*) or cosmic pluralism is commonly used to describe ideas in which the existence of life on other planets was a central topic; see chapter B.5.

in 1692 as the French General Consul in Egypt, a position which he held until 1708. Some of the data used by de Maillet in *Telliamed* were collected during this stay. His experiences in Egypt were laid down in his *Description de l'Egypte* (De Maillet 1735), which was also published by Le Mascrier. During this time de Maillet was chosen by the king of Egypt as his personal envoy to Ethiopia. Although he could not complete this mission, he wrote a text entitled *Mémoires d'Éthiopie.*[28] Between 1708 and 1715 he was consul in Livorno, and from 1715 to 1720 he was *inspector des établissements français dans le Levant et sur les côtes de Barbarie*. It is not known where de Maillet was and what he did between 1708 and 1712 (Rothschild 1964, 352). He did a last trip to Egypt in 1718. During an epidemic in Marseille he went to Paris in 1720, where he stood until 1721. Afterward he went back to Marseille, where he died in 1738 at the age of eighty-two during the preparation of the prints of *Telliamed*.

De Maillet's book *Telliamed* is based on manuscripts, the first draft was probably written during his stay in Egypt between 1692 and 1718.[29] Copies of this manuscript were distributed clandestinely in France for nearly twenty years (Malesherbes 1798, vol. I, 222-224).

The printed versions of *Telliamed* appeared after de Maillet's death. The first edition was published 1748[30] in Amsterdam under following title:

Telliamed, ou entretiens d'un philosophe indien avec un missionnaire français sur la diminution de la mer, la formation de la terre, l'origine de l'homme, etc.[31]

The second edition was published 1749 in Basel. It has the same title and the editor's initials as the first one. Apart from small orthographic variations and stylistic variations, this edition

[28] This was added to Jerónimo Lobo's book *Relation historique d' Abissine* (Lobo 1728).

[29] According to Cohen (1993, 63-64), the first draft was written in 1714. In subsequent years, the manuscript was substantially modified, mainly as a result of investigations and observations carried out in the years de Maillet spent in Marseille, in coastal areas of the Provence, and in the Paris basin (Neubert 1920). Although the original draft is probably lost, several copies of the manuscript are known – Cohen (1993, 59) listed 12 copies. According to Fritz Neubert, who meticulously compared the text of the three editions with the text of five manuscripts, the copies can be divided in two groups. The oldest group (two copies) were written between 1722 and 1725; the second group (three copies) were written between 1725 and 1729. Through the comparison with the printed books Neubert could also reconstruct a third, extended version of the manuscript, which was written around 1731/1732 (Neubert 1920, 207).

[30] Isidore Geoffroy Saint Hilaire (1859, 385) stated that *Telliamed* was already printed in 1735, information that was occasionally adopted by other authors (Huxley 1878, 748; Kohlbrugge 1912, 506). As stated by Neubert (1920, 22-23), this claim is quite unfounded. It is possible that these authors confused *Telliamed* with de Maillet's *Description de l'Egypte,* which was published in 1735.

[31] The editor's name is not given. This sentence follows the title*: Mis en ordre sur les Mémoires de seu M. de Maillet Par J. A. G.***.* These are the initials for Jean Antoine Guer (1713-1764), a writer and lawyer.

is quite similar to the first one. The main divergence is the deletion of some parts.[32] The third, final and most relevant edition was published in two volumes in 1755 in The Hague.[33] This final edition is relevant, because it displays many additions, references, footnotes, and the only available biography of de Maillet. The name of the author is finally mentioned by the editor, Le Mascrier.

The first edition was probably used for the English translation published in London in 1750 (two different imprints with different title pages are known); this work was reprinted in Baltimore in 1797. Contrary to early statements[34], other editions are unknown. The historical-critical edition of *Telliamed* is the annotated and introduced English translation by Albert V. Carozzi (De Maillet 1968). In this work, Carozzi used, acknowledged and complemented the research carried out by Fritz Neubert to reconstruct de Maillet's original manuscript. The annotations to this work are based on an extensive study of the literature. Carozzi's work played an important role in today's positive evaluation of de Maillet's geological investigations.

The printed editions were altered through several modifications by de Maillet's friend Le Mascrier[35] in an attempt to reduce the dangerous character of the book. De Maillet himself tried to avoid a direct confrontation with Christian dogma. As he believed that he could not avoid mentioning some biblical topics, he accomplished this in a self-protecting way, however without making concessions to his system (Carozzi in De Maillet 1968, 10; Neubert 1920, 154-171). When Le Mascrier edited the work, he did it with the purpose to present *Telliamed* as an inoffensive system, compromising to a high degree de Maillet's original thoughts (see below). In fact, as Neubert [1920, 171] states, de Maillet's system in the printed versions is characterized by a much milder style than the system originally presented in the manuscripts; it is doubtful that de Maillet would agree with these posthumous changes. The

[32] At the end of the book, some text-parts that appeared in the first edition, vol. 2, pages 208 to 230 are missing. Also in the *Préface* there are some small deletions, as pointed out by Neubert (1920, 28).
[33] It has the same title as previous editions but followed by a different sentence: *Nouvelle édition, revue, corrigée et augmentée sur les originaux de l'auteur, avec une vie de M. de Maillet*. No editor is mentioned. This edition is known in two different imprints with different title pages and pagination (in the second imprint the dedication is paginated with Roman numerals, the biography of de Maillet with Arabic numerals; in the first imprint all pages are with Arabic numerals).
[34] For instance, Krause (1880, 108) mistakenly mentioned a *Telliamed*-edition published 1746 (the first edition was published 1748); Thienemann's (1909, 227) mentions an edition published in 1750 in The Hague, he probably meant the third edition published in 1755; Kohlbrugge (1912, 510) mistakenly mentioned the Basle-edition published 1740 instead of 1749; however, this was a typographical error, since in another place (Kohlbrugge 1912, 510, footnote 32) he gave the correct information.
[35] This was recognized already by Malesherbes (Malesherbes 1798, vol. 1, 224)

three editions of *Telliamed* appeared after de Maillet's death, without his official permission (Neubert 1920, 27).

As explicit in the subtitle of *Telliamed*, de Maillet's system is presented as conversations between an Indian Philosopher and a French Missionary on the diminution of the sea, whereby de Maillet's ideas are placed in the mouth of the Indian philosopher Telliamed (an anagram of de Maillet's surname). De Maillet regarded the whole universe as a dynamic, ever-changing system. Using Descartes' scheme of vortex (*tourbillions*)[36], de Maillet envisaged the celestial bodies as imbedded in an infinite cyclic process, passing through dark and luminous phases. In the dark phases they may become inhabited, in the luminous phases they are transformed into suns. In de Maillet's system, the earth was originally covered with water. When the water gradually evaporated – a process that began at least 2 billion[37] years ago and is still in progress–, the conditions on the planet became favourable for the development of life. De Maillet assumed that delicate and minute "seeds" of everything which can live are distributed in the whole universe; these seeds rained down on our planet and developed to living creatures in the shallow water sediments, whereby the heat radiated from the sun played an important role (De Maillet 1755, vol. II, 261-274). With the further diminution of the ocean and the subsequent formation of mountains, some organisms eventually colonized the continents and adapted to the new environment. He assumed that every species of land organism evolved from an aquatic counterpart - for example, different species of terrestrial plants originated from aquatic plants (De Maillet 1755, vol. II, 161-162), lions originated from sea-lions, cows from sea-cows, birds from flying fishes, man from mermaids and mermen (De Maillet 1755, vol. II, 162-237). De Maillet's evolutionary scheme implies that secondary aquatic animals (like cetaceans) did not evolve from terrestrial organisms, but emerged primarily in water – a concept that became outdated after the publication of Darwin's *Origin of Species* in 1859.

[36] The Cartesian vortices were popularized by Fontenelle in his *Entretiens sur la pluralité des mondes,* first published in 1686. However, despite this use of Cartesian terminology, Marsak (1959) pointed out that Fontenelle was not a Cartesian, as Fontenelle rejected Descartes' metaphysics and method.

[37] The published versions of *Telliamed* diverge considerably concerning the temporal framework in which the earth was subjected to transformation. For instance, De Maillet's original statements about the diminution of the sea in the past two billion years (De Maillet 1968, 181) respectively about the stars not existing longer than two billion years (De Maillet 1968, 182), as given in the manuscripts, were or deleted or reduced to "two million years" by Le Mascrier (De Maillet 1755, vol. 2, 134, 137) in the printed versions of *Telliamed*. These changes were a hopeless attempt to reduce the difference between de Maillet's time scale and the belief of the world being created in the year 4004 B.C., as calculated from Biblical sources by the Irish scholar and theologian John Ussher in his *Annales Veteris Testamenti, a prima mundi origine deducti* published in 1650. This chronology was used in many editions of the Bible (see Gould 1993, 181-193).

We do not know which works de Maillet might have consulted during his stays in Egypt. He could theoretically have borrowed the idea of organismic transformation and natural selection expressed by Islamic scholars.[38] However, I argue that de Maillet's main inspiration came from two sources: on the one hand, he was influenced by ideas of classical authors, who formulated different concepts of species change (such as those of Anaximander and Lucretius, see below). On the other hand, he developed a concept for the development of the universe and the planets and transferred it to the realm of organismic world.[39]

The Greek philosopher Anaximander (ca. 610-546 BC)[40] and the Roman poet Titus Lucretius Carus (ca. 99-55 BC)[41] are often mentioned in the traditional debate on "Darwin's precursors". Anaximander, the second of the early Ionian philosophers, envisaged a scenario in which first organisms emerged in the moisture and subsequently on dry land:

> The first animals were generated in the moisture, and were enclosed within spiny barks. As they grew older, they migrated onto the drier land; and, once their outer bark was split and shed, they survived for a short time in the new mode of existence. (from Toulmin & Goodfield 1977, 36)

The whole process described above strongly remembers an analogy of the metamorphosis a holometabolous insect undergoes when marked changes take place before a chrysalis is transformed into an imago. Moreover, he equated the pupa and the insect with a vertebrate appearing from a structure analogous to a sea-urchin or a chestnut (when protected by a spiny

[38] De Maillet quoted Islamic scholars, like Abu Yahya Zakariya' ibn Muhammad al-Qazwini (De Maillet 1968, 192-193), a Persian author (1203-1283) who wrote an influential cosmography; for an Arabic translation see el-Cazwini (1967); see Qazwini (1986) for a partial and el-Cazwini (1994) for a full German translation. Several copies of this work survived. I recently acquired a fragment of a manuscript that might be attributed to this author or written in the same tradition as al-Qazwini's cosmography (the fragment is still waiting for the evaluation by an expert). Ideas evoking species change can for instance be found in the ninth century *Book of Animals* by the Mu'tazili philosopher al-Jâhiz (c. 776-869); see quotation in Zirkle (1941); see Nabielek (1998, 110-140) for an excellent review on biology in medieval Arab-Islamic world. I am not aware of a specific aspect of de Maillet's evolutionary ideas which indicates that he was influenced by al-Jâhiz; see also footnote 130.

[39] Similarly, Robert Chambers was strongly influenced by the Copernican revolution. In several parts of his *Vestiges of the Natural History of Creation* he discussed the topic plurality of worlds. Following passage is insightful concerning his views on Deism in the context of the plurality of world-discussion, which is characteristic for several early authors:

> More than this, the fact of the cosmical arrangements being an effect of natural law, is a powerful argument for the organic arrangements being so likewise, for how can we suppose that the august Being who brought all these countless worlds into form by the simple establishment of a natural principle flowing from his mind, was to interfere personally and specially on every occasion when a new shell-fish or reptile was to be ushered into existence on one of these worlds? Surely this idea is too ridiculous to be for a moment entertained. (Chambers 1844, 154)

[40] On Anaximander see Erhard (1940), Loenen (1954), Schultze (1877)and Toulmin and Goodfield (1977).

[41] On Lucretius' atomism and concept of "germs", see chapter B.3. On concept of species changes in classical authors see also Zeller on "Greek precursors of Darwin" (the translated title) (Zeller 1879).

shell). In the following passage he tried to explain the origin of humans, which he envisaged as emerging from a fish-like animal:

> Man, to begin with, was generated from living things of another kind, since, whereas others can quickly hunt for their own food, men alone require prolonged nursing. If he had been like that in the beginning, he would never have survived. Thus men were formed within these [creatures, comparable with fishes] and remained within them like embryos until they had reached maturity. Then at last the creatures burst open, and out of them came men and women who were able to fend for themselves. (from Toulmin & Goodfield 1977, 36)

There are several similarities between Anaximander's and de Maillet's[42] scenarios describing the plasticity of organismic phylogenetic development. Both authors referred to water as a place where important phases of the development could take place, both envisaged organisms passing from water (or wet terrain) onto dry land to complete or continue the phylogenetic changes; both authors used (implicitly or explicitly) analogies between phylogeny and ontogeny. The last point is well illustrated in following passage, where De Maillet tried to convince his readers that evolutionary process was a reasonable phenomenon:

> The transformation of a silkworm or of a caterpillar into a butterfly would be a thousand times more difficult to believe than that of fish into birds if this metamorphosis did not occur daily before our own eyes, or if it were told to us in a part of the world where it was unknown. (De Maillet 1968, 188)

De Maillet's passage on the transformation of a fish into a bird (see below) was only one of his attempts to explain all terrestrial organisms as evolving from aquatic counterparts. He introduced this concept by quoting verbatim following sentences:

> "The sea contains fishes of almost all the shapes of land animals, and even of birds. It includes plants, flowers, and some fruits: the nettle, the rose, the carnation, the melon, the grape have their equivalent in there". (De Maillet 1968, 187)

The verbatim quotation, according to a footnote in *Telliamed* (De Maillet 1748, 138) is from "Sorel, fol. 149", which refers to Charles Sorel (ca. 1602-1674), a French writer and historian. (De Maillet also refers to this author in another part of *Telliamed*.)[43] The above passage is not

[42] Another naturalist who was probably influenced by Anaximander is Oken (see Appendix A) with his speculations of aquatic human babies.

[43] After listing several arguments towards human's origination from water, de Maillet referred to the view of Thales and Anaxagoras, who believed that water was the first principle of all things, and the ideas proposed by Anaximenes of Miletus (c. 585- c. 528 BC), who believed that not water but air was this primary substance. De Maillet's argued that Anaximenes view "amounts to the same doctrine, because, according to Sorel, water is

really verbatim, but a summary of Sorel's sentences from *La science universelle*, 4 vols, first published 1634.[44]

However, the analogy between aquatic and terrestrial organisms can be found in earlier texts, and it is possible that Sorel borrowed it from Pliny the Elder[45] (AD 23- AD 79), who wrote in his *Naturalis historia*:

> There are however a considerable number of these [creatures of the seas, rivers and ponds] that are larger even than land animals. The obvious cause of this is the lavish nature of liquid. Birds, which live hovering in the air, are in a different condition. But in the sea, lying so widely outspread and so yielding and productive of nutriment, because the element receives generative causes from above and is always producing offspring, a great many actual monstrosities are found, the seeds and first principles intertwining and interfolding with each other now in one way and now in another, now by the action of the wind and now by that of the waves, so ratifying the common opinion that everything born in any department of nature exists also in the sea, as well as a number of things never found elsewhere. Indeed we may realize that it contains likenesses of things and not of animals only, when we examine the grape, the sword-fish, the saw-fish, and the cucumber-fish, the last resembling a real cucumber both in colour and scent; which makes it less surprising that in cockle-shells that are so tiny there are horses' heads projecting. (Pliny 1967, book IX, 165, English translation by H. Rackham)

De Maillet's decision to mention mythological creatures (e.g., mermaids) as real organisms and distantly related organisms as descending from each other (birds from flying fishes, lions

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only a condensed air and air a rarified water, since there is air in water, and water in air, and in both a terrestrial matter which becomes visible in the sediment" (De Maillet 1968, 220). According to Carozzi (in De Maillet 1968, 390, note 67), this reference is in Volume I, pp. 328-331; I could not find this topic discussed in these pages, but I consulted another edition (from 1637) and I still did not go through the whole work.

[44] The passage reads as follows:

> Quant à la figure des poissons, elle tire sur la longueur; mais il y en a de ronds & de plats, selon que leur matiere s'est ramassee ou dilatee. Il y en a presque aussi de toutes les figures des animaux terrestres, comme des chiens, des chevaux, des veaux, des beliers, des herissons, des Elephans & autres, comme aussi de plusieurs oyseaux; & mesme quelques Plantes, quelques fleurs, & quelques fruicts y trouvent leur ressemblance, comme l'Ortie, la Rose, l'Oeillet, le Melon, & le Raisin; dont la raison est à mon avis, qu'il y a de certaines reigles pour le meslange des matieres qui s'observent par tout, & qu'estans semblables dans les eaux comme sur la Terre, elles ont produit des animaux qui sont près que pareils, & qui n'ont autre diversité de formes que ce qui convenoit à leur Nature aquatique, comme d'avoir des nageoires au lieu de pieds, d'estre aussi autrement couverts, & d'estre dans l'interieur d'une constitution plus humide. (Sorel 1647, vol. 2, 228-229)

Sorel then explained that organismic diversity is greater in the sea than on land, because the movement in water facilitates the production of forms (Sorel 1647, vol. 2, 229).

[45] As stated above (footnote 43), I still did not investigate in detail the four volumes of Sorel's *La science universelle*. However, in another work by Sorel - *De la perfection de l'homme* – he mentions Pliny the Elder (Sorel 1655, 14). In this book, Sorel discussed the ancient question if humans are essentially perfect – his opinion – or deficient creatures.

from sea-lions) was obviously influenced by the idea of aquatic counterparts for land creatures. He and other proponents of pre-Darwinian evolutionary concepts[46] seemed not to realize that humans have the tendency to name newly discovered organisms by using vague similarities between these and those already known. The idea of counterparts was also expressed by other early authors[47] and the tradition of finding aquatic counterparts to terrestrial mythological creatures is still cultivated in non-scientific circles.[48]

B.3 De Maillet's inclusion of mythological creatures in evolutionary ideas

De Maillet's view on the organismic world was highly exotic, as he was quite convinced of the existence of several mythological creatures and did not hesitate to integrate them into his system. He saw among others that the following creatures were witnessed by many credible people: tritons or sea men (De Maillet 1968, 191-200, 212-221), hairy savage man (De Maillet 1968, 200-202), men with tails (De Maillet 1968, 202-206), and giants and dwarfs (De Maillet 1968, 207-211). Some early and modern historians or naturalists[49] are convinced that this aspect of de Maillet's evolutionary system is incompatible with a scientific discourse, and this opinion is partially responsible for the underreporting of de Maillet's ideas in biological textbooks (see chapter B.4.3).

At first view, de Maillet's integration of mythological creatures seems to be a remarkable regression to ancient[50] and medieval zoology. De Maillet did not have problems finding

[46] See for example similar erroneous views on terrestrial animals evolving from secondary aquatic organisms by Chambers and Goethe (chapter B.3).

[47] See the picture of an aquatic unicorn (Jonstonus 1657, table x), also depicted in http://photos1.blogger.com/blogger/1717/1584/1600/Johnston%20a.jpg This unicorn with webbed hind limbs remembers mythological hybrids, for instance the seahorse, often depicted ridden by the Roman god Neptune.

[48] The tendency to see counterparts between aquatic and terrestrial organisms can be found in the area of cryptozoology, a field attracting layman and – curiously enough – single trained biologists interested in bringing mythological creatures back into the realms of reality. It is remarkable to see how cryptozoologists react rapidly to data published in scientific literature. An interesting example is supplied by an aquatic counterpart of Bigfoot (or Sasquatch), the North American version of the medieval wild man. Only one year after Alister Hardy published his arguments towards the aquatic hypothesis on human evolution (Hardy 1960b), speculations on a semi-aquatic Bigfoot were expressed by the biologist and cryptozoologist Ivan Sanderson (see also Krantz 1992, 51, a palaeoanthropologist and also cryptzoologist; 1961, 141). Similarly, immediately after the publication of the first description of swimming apes, showing swimming leg movements not unlike those of the human frog-kick (Bender & Bender 2013), a statement was published online recalling that bigfoot has been already observed swimming on different occasions, and in at least one case using a frog-like technique while catching salmon underwater; see http://bigfootevidence.blogspot.ch/2013/08/yes-bigfoot-can-swim-scientists-prove.html and http://bigfootevidence.blogspot.ch/2011/12/did-you-know-that-bigfoots-can-swim.html . See also the crytozoological book by Cazottes and de Sarre (2006, 81-130).

[49] On the early and modern reception of de Maillet's evolutionism see chapter B.4.

[50] However, this does not applies to Aristotle (384 – 322 BC). Although Aristotle mixed observations of nature with narrative elements in his zoological works (e.g., *Historia animalium* IX, 32; 619a8-619b12), he was, compared with Pliny (see below), rather cautiously concerning mythological creatures. Why did later authors not follow him on this point? Until the translation of Aristotle's works on zoology in the 13th century, Aristotle's

sources for imaginary organisms, as these stories were evidenced in several zoological works: (a) *Physiologus* (Anonymous 1992; Anonymus 1964), a text with moralized beast tales that were very popular in the Middle Ages (Henkel 1976; Meyer 1884; Steiger 1964); (b) the encyclopedia *Naturalis historia* by Pliny the Elder (Pliny 1967) published circa AD 77-79 (Borst 1995a); (c) the *Buch der Natur* by Konrad von Megenberg (1897), first published between 1348 and 1350; or (d) Sebastian Münster's *Cosmographia*, first published in 1544 (Münster 1978). Even Conrad Gessner and Ulisse Aldrovandi, both often regarded as founders of modern zoology, were not successful in breaking the medieval tradition of depicting legendary creatures in zoological works. (However, it is certainly too simple to regard these authors as uncritical just due to their inclusion of fantastic creatures.)[51] Further sources for the belief of mythological creatures[52] were fictive or partially fictive travel literature, e.g., *The Voyage of Saint Brendan* (Brandan 1994), John Mandeville's *Itinerarius* (ca. 1485) along with other mariner's stories often had accounts of mermaids[53], and imaginative interpretations of fossil evidence (see Abel 1939). Yet others drew illustrations of abnormalities in the physiological development of animals and humans (Schumacher 1995; Sonderegger 1927), and even more, fantastic stories of interspecific transformation of

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zoology was known only from other authors, such as Pliny and Isidor von Sevilla (Ribémont 1997), who did not in all cases acknowledge Aristotle's authorship (Obermaier 2009, 13). As Carl Meyer (1884) stated, Aristotle's critic views and methods did not belong to the public domain of naturalism in the antiquity. In fact, Aristotle's studies on animals "were not superseded until more than two thousand years after his death" (Barnes 1982). Ernst Mayr summarized the development of biology in the centuries after Aristotle: "As a broad generalization one can probably say that the level of natural history went steadily downhill after the death of Aristotle. [...] In the ensuing period animals were written about not for the sake of providing knowledge about them but for the sake of moralizing; they became symbols" (Mayr 1982, 153).

[51] In his monumental encyclopaedia *Historia animalium*, first published 1551-1558, Gesner has confined himself to few examples, which he often commented on critically [Ley, 1929;Friedrich, 1995;Bäumer, 1991, 42-73;1996]. Some of the negative evaluation of Gessner by modern historians is related to his work *Thierbuch*, the German translation of *Historia animalium* published in 1563 - a summary of the two first volumes of *Historia animalium*. As Bäumer (1991, 65) pointed out, Gessner gave in this abridged version the impression that he was very uncritical of mythological creatures, as several of his critical statements published in the original edition were absent. The reader of the German abridged edition was no longer able to distinguish clearly between imaginary and real organisms, which had been possible in the original edition. In fact, the German edition followed more the traditional concept of popular works written for entertainment, for instance in the herbals. Similarly, Aldrovandi is sometimes considered as uncritical towards mythological creatures. However, as observed by different authors (Bäumer 1991, 103; Nordenskiöld 1926, 97) this is unjustified, as most of Aldrovandi's works were published after his death and he cannot be responsible for uncritical publications of his works. One important aspect of the parallel use of mythological and real creatures is proposed by William B. Ashworth Jr. For him mythological creatures are the expression of the inability of naturalists in 16th century to account for different aspects of human experience: Animals in ancient zoology are "just one aspect of an intricate language of metaphor, symbols, and emblems. This 'emblematic world view', as I choose to call it, was the single most important factor in determining the content and scope of Renaissance natural history" (Ashworth 1990, 305); see also Ashworth (2003).

[52] The topic "legendary creatures" were investigated by several authors (Armour 1997; Baltrusaitis 1985; Cherry 1997; Mode 1977; Obermaier 2009; Schöpf 1988; Wunderlich 1999).

[53] The belief on legendary aquatic humanoids was topic of several investigations (Benwell & Waugh 1961; de Castro Pires de Lima 1952; Duchet 1995; Heinisch 1981).

organisms (see for example the stories about the origin of birds or mammals from plants in Appendix A) or on the creation of new organisms through the mating of two distantly related species.

The dissemination of ideas on fictional creatures was not discouraged by works published in the 16th and 17th centuries that allegedly described from nature spices, medicines, plants and animals found by explorers during the European expansion into tropical countries. A good example is the book entitled l'*Histoire générale des drogues, traitant des plantes, des animaux et des minéraux, etc.*, by Pierre Pomet (first published 1692) and commonly considered as the most complete work in this literary genre at that time. In his book, Pomet described and depicted not only real organisms, but also mythical creatures, such as several species of unicorns[54] (Pomet 1987, 471-472). This information was mixed into the widespread superstitions of the Middle Ages and following centuries (Meyer 1884). These stories were gradually recognized by educated people[55] as the product of imagination, especially after the publication of Thomas Browne's *Pseudodoxia Epidemica or Enquiries into very many received tenets and commonly presumed truths* (1658).

As we can see, de Maillet's belief in mythological creatures seems to be exactly the opposite of what might have been expected from an enlightened author of 18th century. This point seems to justify the commonly[56] expressed opinion that de Maillet's system is closer to

[54] To give credibility to such stories, early authors frequently referred to former works. In this case, Pomet referred to Jan Jonston's *Historiæ Naturalis de Quadrupedibus* (Jonstonus 1657). This work, first published in 1650, although not well appreciated by historians of science, is sporadically regarded as a watershed publication. Michel Foucault suggested that Jonston's work symbolizes a break with earlier Renaissance natural history, an opinion that is endorsed by William B. Ashworth Jr (2003); Ashworth Jr discusses the role Jonston's encyclopaedia played in the demise of what he called "emblematic natural history" (see footnote 51). On Jonston's picture of an amphibian unicorn, see footnote 47.

[55] The belief in mythological creatures did not disappear completely from natural sciences with the consolidation of the scientific method in the Age of Enlightenment. Today, the belief in such creatures is mostly associated with a small group of "cryptozoologists". They follow the footpaths of the zoologist Bernard Heuvelmans (1995) in their hopeful efforts of prove the existence of "cryptids" like Bigfoot, Yeti, the Monster of Loch Ness, the Saci Perere, or mermaids; see footnote 52 for some references.

[56] There are some remarkable exceptions. The criticism of de Maillet as a propagator of natural philosophical fantasies was doubted by Kohlbrugge (1912). This article is to my knowledge the first extensive publication on de Maillet's system in which the merit of the French naturalist is fully acknowledged. Kohlbrugge is sometimes quoted by modern historians in a negative context in connection with his paper *War Darwin ein originelles Genie*? In this work he pointed out an astonishing number of scholars who mentioned evolutionary ideas before 1859 in an unfair attempt to accuse Darwin of being superficial in his acknowledgment of precursors of evolutionary ideas and to revile Darwin's achievements as an evolutionist (Kohlbrugge 1915). However, Kohlbrugge's work as historian of science should not be reduced to this single publication. Similarly, Tschulok, a specialist on Lamarck's work (and rarely quoted by de Maillet's experts) aptly argued that the usual evaluation of de Maillet's system as is strongly biased. Most early critics of de Maillet, according to Tschulok, come from authors who probably never read *Telliamed* in the original (Tschulok 1938). See also chapter B.4.3 for other benevolent opinions about this book.

medieval superstition than to a scientific revolution. However, this evaluation failed to grasp the full significance of his work and its influence on other naturalists. This influence can be established by referring to following facts. For example, the evidence supporting the extraordinary dissemination of printed versions of *Telliamed* was provided in the early 20th century by Daniel Mornet,[57] who investigated 500 catalogues held by French public libraries in the 18th century. By using the number of copies of books on natural sciences to estimate the popularity of these works he came to the remarkable result of *Telliamed* ranking number six [Mornet, 1911, 248-249]: 1. Buffon (220 copies), 2. Pluche's *Spectacle* (206), 3. Valmont de Bomare's *Dictionnaire* (93), 4. Dezallier d'Argenville's *Ouvrages de notre bibliographie* (86), 5. Réamur's *Mémoires* (82), and 6. de Maillet's *Telliamed* (72 copies).

Although the sixth rank is quite impressive, it still does not accurately reflect the influence of *Telliamed* on the scientific discussion of this time, as Mornet's investigation did not make a distinction between the works according to the purposes for which they were written. This differentiation is important, as books of popular science and references books should be expected to be overrepresented in library catalogues. For instance, the books written by Buffon (first rank), de Bomare (third), d'Argenville (fourth) and Réamur (fifth) are encyclopaedias or dictionaries and therefore indispensable for libraries on natural sciences in this time. Noël-Antoine Pluche's *Spectacle de la nature* [Pluche, 1752, first publ. 1732], ranked second, is a work on the popularization of natural sciences, a category which does not apply to *Telliamed*.

This might sound surprising, as *Telliamed* is often referred to as a "work of fiction" [Mayr, 1982, 311], possibly because its content is given in dialog form. However, the dialog form was not unusual in this time for the presentation of scientific ideas.[58] The same form already had been used by de Maillet's friend Fontenelle in his *Entretiens sur la pluralité des mondes* [1780, first publ. in 1686], in which the author defend the Copernican astronomy and the Cartesian theory of vortices and discussed aspects of the plurality of worlds; the work was

[57] The popularity of *Telliamed* in 18th and early 19th century was stressed by different authors (Kohlbrugge 1912; Neubert 1920; Quatrefages 1870; Tschulok 1938).

[58] See *Dialogo sopra i due massimi sistemi del mondo tolemaico, e copernicano* (1970, first ed. 1632) by Galileo Galilei, *Entretien d'un philosophe chrétien et d'un philosophe chinois sur l'existence et la nature de dieu* by Nicolas Malebranche (1986, first ed. 1707) or *Entretien d'un philosophe avec la maréchale de *** by Denis Diderot (1905, first ed. 1776)* See Kalverkämper (in http://edoc.hu-berlin.de/humboldt-vl/172/kalverkaemper-hartwig-15/PDF/kalverkaemper.pdf) for the dissemination of the use of the dialog form in 17th and 18th century science.

certainly written to entertain the public.[59] Contrary to this, *Telliamed* was conceived as a scientific discussion on geology and the plurality of worlds, with sophisticated arguments against both the dogma of the immutability of species as well as James Ussher's estimation of the age of world (4004 BC). A further alleged similarity between *Telliamed* and Fontenelle's work is the division of six conversations. However, this division cannot be attributed to de Maillet, as it was introduced by Le Mascrier[60], among others as an attempt to make *Telliamed* superficially similar to Fontenelle's famous book and to allude to the Genesis creation narrative – both components used by Le Mascrier to reduce the danger of de Maillet's system [see Carozzi in De Maillet, 1968b, 26-27]. *Telliamed* was not just used to fill gaps on French library shelves – the book was widely consulted. Its influence can be identified in several works on geology and also crucial to the emergence of transformist ideas proposed before 1859.The early and modern discussion on the value of de Maillet's system will not be reviewed in detail here.[61] I will restrict myself to some still widely ignored evidence on de Maillet's influence on proponents of transformist ideas in the early 19th century, and some typical observations expressed by modern biologists.

Among the few early authors who mentioned de Maillet positively was the German protestant theologian and geologist Johann Georg Justus Ballenstedt (1756-1840). In his widely ignored treatise on geology and transformism, *Die Urwelt oder Beweis von dem Daseyn und Untergange von mehr als einer Vorwelt* (The primeval world or proof of the existence and extinction of more than one prehistoric world), Ballenstedt wrote about gradual evolutionary changes in living organisms, postulating that geological facts demonstrated that the earth was much older than commonly believed in this time (Ballenstedt 1819, vol. 1, 9). In an appendix entitled *Ueber die Existenz der Wassermenschen* (On the existence of aquatic men) he mentioned the possibility that aquatic men are real organisms and not fables. He quoted a long

[59] On the relationship between de Maillet and Fontenelle / Le Mascrier see Benitez (1980; 1984); on the place of Fontenelle's *Entretiens* in the plurality of worlds discussion see Shackleton (1955).

[60] The dedication of the book to Cyrano de Bergerac, also inserted by Le Mascrier, is certainly another aspect of his strategy to present *Telliamed* as a hybrid work situated between science fiction and science; on Bergerac see Dübi (1906). Voltaire's statement on this dedication (quoted below, chapter B.4.3) shows that the strategy was partially successful; see also Andrés (1841, 420), who wrongly assumed that the dialog form was proposed by Le Mascrier, but did not recognize that the dedication to Bergerac was inserted by Le Mascrier ; see also Krause in Lang (Krause in 1878, 261), who defended what he believed to be *de Maillet's* mention of Bergerac in *Telliamed*. Both historians of the evolutionary thought before 1968 (see, e.g., Crocker 1959, 123) as well as modern authors of popular accounts on history of evolutionary thought are often not aware on the amendments of *Telliamed* by Le Mascrier (Milner 1990, 127); this problem often rises when *Telliamed* printings from 18th century are consulted without the help of textual work.

[61] Some aspects of the reception of de Maillet's biological ideas are discussed below (chapter B.4) and several other investigations (Bender 1999b; Benitez 1980; 1984; 1989; 1990; 1993; Carozzi 1968; Charbonnat 2010; Cohen 1993; Dalrymple 2004; Carozzi in De Maillet 1968; Jordan 1914; Kohlbrugge 1912; Lang 1878; Neubert 1920; Tschulok 1938).

passage from *Telliamed*, which he knew only from secondary literature[62] (Ballenstedt 1819, 223-228).

De Maillet was also quoted by James Burnet (sometimes spelled Burnett), Lord Monboddo (1714-1799) in support of his ideas on the nature of men. Monboddo argued that a definition of man does not require the ability to speak, but the ability to make and use tools. In an attempt to blur the differences between men and other animals, he exaggerated the animal characteristics of humans and the human features of apes. In several works[63] he developed his hypothesis that the "Orang Outang" is not an ape, but a human. In 18th century, this term did not necessarily refer to the orangutan, *Pongo pygmaeus.*[64] Until the end of 18th century, "ape" was not only used indiscriminately for African great apes and Southeast-Asian orangutans, but also for all kind of real or mythological "wild man of the woods" (Brown 2000; Corbey 2005; Nash 1995; Spencer 1995; see Tinland 1968, 89-129). In his *Of the Origin and Progress of Language* Monboddo argued that some ancient and modern men lived "in the brutish state, without arts or civility" (Monboddo 1773, vol. 1, 217).[65] In a second edition of this work Monboddo incorporated an essay on the Orang Outang (Monboddo 1774).

In this edition he stated that Orang Outans is "a barbarous nation, which has not yet learned the use of speech" (Monboddo 1774, vol. 1, 270). He saw the expression "not yet" as justified, since the organic pre-conditions for the development of language are given in this creature. Referring to Buffon's work, he argued that the brain of Orang Outans, the tongue and other "organs of pronunciation" are "the same as those of man" (Monboddo 1774, vol. 1,

[62] He quoted de Maillet from Poncelin (1801, vol. 1, 215-218).

[63] His arguments are developed in *Antient Metaphysics* (six volumes, 1773-1799), *Of* the *Origin and Progress of Language* (six volumes, 1773-1792) and several unpublished manuscripts (quoted in Barnard 1995).

[64] It was employed by the Dutch physician Nicolaas Tulp (1593-1674) in chapter 56 of his *Observationes medicae,* first published in 1641 (Tulp 1716, 270-277). In this work, Tulp presented the first scientific description and the first illustration of an anthropoid ape from Angola, probably referring to a common chimpanzee. Tulp used the term Orang Outang as a generic name, similar to today's term "ape".

[65] In other parts of his work Monboddo had already given "sundry examples of solitary savages who have been found at different times, in different parts of Europe, without language or arts of any kind, and even without the erect form" (vol. 1, 237). For instance, referring to Diodorus Siculus, Monboddo gave an account of the "fish-eaters", a group who lived "near the strait which joins the Indian Ocean to the Red Sea or Arabian gulf, upon the Asiatic side" (vol. 1, 239). According to Diodorus (Siculus 1953, book III, 15-17), the fish-eaters or *Ichthyophagi* lived almost entirely on fishes; see full quotation in Appendix A. The classification of humans in categories according to their staple diet or habitat was also used by William Pownall (1722-1805), Governor of Massachusetts from 1757 to 1760, in a book *An Antiquarian Romance*, first published in 1795. In this account of the history of the European races based upon ancient authors, Pownall described first humans as "woodland-men" or "Sylvan men" who did not have the same opportunities to become as prolific as "land-workers" (see quotation in Appendix D). He also wrote about "watermen" and "fishermen" (pp. 30-32) and fisher-tribes (p. 115). The strong connection between primeval men and a specific landscape is the most important feature of early and modern savannah hypotheses and their deviations (e.g., aquatic hypotheses, woodland or mosaic landscape-hypotheses) (see Bender et al. 2012).

271). As part of his argumentation on the apes' potential or actual ability to speak, he quoted a passage from the English translation of *Telliamed* published in London in 1750, in which de Maillet reported on the existence of "savage-men" – actually orangutans.[66] Monboddo wrote:

> Lastly, I say, that, in certain parts of the world, this wild man of the woods is to be found with some use of articulation. This is attested by Mr Maillet, the author of the Description of Egypt, who, in a work of his, entitled Telliamed, has collected a great many curious facts concerning the varieties of our species. (Monboddo 1774, vol. 1, 301-302)

This explicit mentioning of de Maillet's ideas by early evolutionists is rather exceptional, since several early passages taken out of *Telliamed* were rarely acknowledged by early naturalists. An example from the non-scientific literature is supplied by the French lawyer, politician and gastronome Jean Anthelme Brillat-Savarin (1755-1826). In his famous book *Physiologie du goût* (first publ. in 1825) he wrote in a chapter on fish and shellfish (very fittingly) as follows: "Some men of learning, but not very orthodox, have maintained that the ocean was the common cradle of every living thing, that even the human race was born in the sea, and that it only owes its present state to the influence of the air and to the habits which it has been obliged to adopt in order to dwell in this new element" (Brillat-Savarin 1884, 119).[67]

Brillat-Savarin's statement summarizes, as stated above, one of the most important and influential elements in the Mailletian system – the idea of aquatic organisms adapting to a terrestrial environment. The description of the transformation of an aquatic organism to its terrestrial counterpart was formulated by Immanuel Kant in § 80 of his *Kritik der Urteilskraft* (Critique of the Power of Judgment), first published in 1790 (Kant 2000). To understand this

[66] Here is the English translation of De Maillet's words:

> Nothing is more common than those Savage-men; in 1702, the *Dutch-East India* Company sent out two Vessels from *Batavia* or the Coasts of *New Guinea*, and the Southern countries, in order to trade and make Discoveries. During that Expedition, which was of no Use, the *Dutch* seized two Male Animals, which they brought to *Batavia*, and which, in the Language of the Country where they were taken, they called *Orangs-outangs*, that is, Men who live in the Woods. They had the whole of the human Form, and like us walked upon two Legs. Their Legs and Arms were very small, and thick-covered with Hair, some of which they also had on the whole of their Body, their Faces not excepted. Their Feet were flat, where they are joined to the Leg, so that they resembled a Piece of Plank with a Baton driven into it. These *Orangs-outangs* had the Nails of their Fingers and Toes very long, and somewhat crooked. They could only articulate Sounds very indistinctly; but were very melancholy, gentle, and peaceable. The one died at *Batavia*, and the other in the Road to *Holland*, whither he was sent as a Curiosity worthy the Admiration of all *Europe*. (De Maillet 1750, 245-246)

[67] „Quelques savants, d'ailleurs peu orthodoxes, ont prétendu que l'Océan avait été le berceau commun de tout ce qui existe; que l'espèce humaine elle-même était née dans la mer, et qu'elle ne devait son état actuel qu'à l'influence de l'air et aux habitudes qu'elle a été obligée de prendre pour séjourner dans ce nouvel élément" (Brillat-Savarin 1848, 64). This work was translated in German by the Swiss-German Darwinist Carl Vogt (1817-1895) (Brillat-Savarin 1888, 70), the same author who translated Chamber's *Vestiges of the Natural History of Creation* to German.

specific passage we have to consider some of Kant's ideas on a gradual approach from one common prototype to another.[68] Kant wrote (translated by Paul Guyer and Eric Matthews):

> The agreement of so many genera of animals in a certain common schema, which seems to lie at the basis not only of their skeletal structure but also of the arrangement of their other parts, and by which a remarkable simplicity of basic design [*Grundriss*] has been able to produce such a great variety of species by the shortening of one part and the elongation of another,[69] by the involution of this part and the evolution of another, allows the mind at least a weak ray of hope that something may be accomplished here with the principle of the mechanism of nature, without which there can be no natural science at all. (AA 5: 418)

Kant was referring to what once was perceived as "analogy of forms" which is often synonymous with the modern concept of homology (without the concept of the evolution of a common ancestor). However, as evident in the following passage, the view of analogy as an abstract schema also could be used in what superficially resemble an evolutionary concept. Kant wrote:

> This analogy of forms, insofar as in spite of all the differences it seems to have been generated in accordance with a common prototype [*Urbild*], strengthens the suspicion of a real kinship among them in their generation from a common proto-mother [*Urmutter*], through the gradual approach [*stufenartige Annäherung*] of one animal genus to the other, from that in which the principle of ends seems best confirmed, namely human beings, down to polyps, and from this even further to mosses and lichens, and finally to the lowest level of nature that we can observe, that of raw matter: from which, and from its forces governed by mechanical laws (like those which are at work in its production of crystals), the entire technique of nature, which is so incomprehensible to us in organized beings that we believe ourselves compelled to conceive of another principle for them, seems to derive. (AA 5: 418-419)

Kant continued with a text which remembers views expressed by antique thinkers, notably by Lucretius in his *De rerum natura*[70]:

> He [*der Archäologe der Natur*] can have the maternal womb of the earth, which has just emerged from a condition of chaos (just like a great animal), initially bear creatures of less

[68] For an in-depth analysis of the topic "Kant as pioneer of evolutionism" see Lovejoy (1959c).
[69] This is basically the Aristotelian view of 'the more and less' expressed in his *De partibus animalium* I 4, 644 a 12-23.
[70] The resemblance to Lucretius' poem (Lukrez 1981) is indicated by following elements: (a) the conditions of chaos in the initial stages of life; (b) the creation of organisms from a mother earth; (c) the mention of nature stopping to produce new forms (which Lucretius presented as an analogy between mother earth and the old organismic mothers; and finally (d) the mentioning of a kind of natural selection and adaptive process (Müller 2003, 305-327; Schoeck 1974).

> purposive form, which in turn bear others that are formed more suitably for their place of origin and their relationships to one another, until this birth-mother itself, hardened and ossified, has restricted its offspring to determinate species that will degenerate no further, and the variety will remain as it turned out at the end of the operation of that fruitful formative power. – And yet ultimately he must attribute to this universal mother and organization purposively aimed at all these creatures, for otherwise the possibility of the purposive form [*Zweckform*] of the products of the animal and vegetable kingdoms cannot be conceived at all. (AA, 5: 419-420)

Kant attached a footnote to the last sentence, where he wrote:

> One can call an hypothesis of this sort a daring adventure of reason, and there may be few, even among the sharpest researchers into nature, who have not occasionally entertained it. For it is not absurd, unlike *generatio equivoca* [aequivoca], by which is meant the generation of an organized being through the mechanism of crude, unorganized matter. It would still be *generatio univoca* in the most general sense of the term, insofar as something organic would be generated out of something else that is also organic, even though there would be a specific difference between these kinds of beings, e.g., as when certain aquatic animals are gradually transformed into amphibians and these, after some generations, into land animals. (AA 5: 419)

Although Kant's text evoking the idea of evolutionism is known among historians of philosophy of 18th and 19th century, this passage is, as pointed out by Lovejoy, "unfortunately, usually quoted with its most important part – an appended footnote –omitted". It comes, therefore, not as a surprise that most experts did not see the stringent similarity between Kant's statement to a transition from aquatic to terrestrial organisms and the main arguments of the Darwinian system.[71]

Another interesting and widely ignored text was written by Johann Wolfgang von Goethe (1749-1832). Goethe wrote on a hypothetical origin of sloths from a "monstrous spirit" (*ein ungeheurer Geist*), similar to a whale (*Walfisch*):

[71] Also Lovejoy did not mention de Maillet in his article on Kant. However, in a recent paper, Peter McLaughlin pointed out this similarity in an article where he argued against the occasionally held idea that Kant should be regarded as a forerunner of Darwin: "Let us first look at the brief speculation on the origin of land animals from sea animals, which Kant derives from [...] *Telliamed*" (McLaughlin 2010, 8). McLaughlin had excellent reasons to mention de Maillet in this context. No other pre-Darwinian naturalist was so strongly akin to the idea of all species of terrestrial organisms evolving from aquatic counterparts as de Maillet. As we will see, this association is so strong that some modern scientists even accused de Maillet as not having been a proponent of an evolutionary system because he put so much emphasis on this transition. As pointed out in chapter B.4.3, this criticism is contestable and belongs to the long tradition of emphasizing single aspects of the de Mailletian system in an attempt to demonstrate that the French naturalist could not be an early propagator of evolutionary ideas.

> One may permit us some poetical expression since prose would in no way be adequate. A monstrous spirit, as one which in the ocean could well show itself as a whale, throws itself upon a swampy, gravelly shore of a torrid zone. It loses the advantages of a fish. It lacks a supporting element to bear its weight – an element which grants the most heavy body ease of movement through the smallest of organs.[72] (Goethe 1954 (1821), I, vol. 9, 247-248) (translated by Astrida Orle Tantillo)

Goethe's evolutionary scenario is very similar to following passage by de Maillet. In his attempt to exemplify the circumstances in which an aquatic organism would leave the water and occupy the land, de Maillet used an analogy between flying fishes and birds and imbedded it in an evolutionary scenario. De Maillet wrote as follows (translation by Carozzi):

> For instance we know that often winged or flying fish, either chasing or being chased in the sea, stimulated by the desire of prey or the fear of death, or perhaps tossed a few feet on the shore by stormy waves, have fallen among reeds or weeds, from which it was not possible for them to resume their flight to the sea, under which circumstances they could have developed a greater facility for flying. Then their fins, being no longer bathed in sea water, were split and became warped by drying. While they found among the reeds and weeds in which they had fallen some food to support them, the vessels of their fins, separated from each other, were lengthened and covered with fringes, or to speak more precisely, the membranes which previously had kept them adherent to each other were metamorphosed. (De Maillet 1968, 187)

De Maillet gave some details of the metamorphosis from flying fish to bird:

> The fringe formed by these warped membranes was lengthened, and the skin of these animals became gradually covered with a down of the same color as the skin, and this down in turn increased, The little wings which they had under their belly, and which like their fins helped them to walk on the sear bottom, became feet and served them to walk on land. Other small changes occurred in their shape. The beak and neck of some were lengthened, and those of others shortened; this was also true for the rest of the body. However, the appearance of the original shape remains in the whole; it is and will always be easy to recognize. (De Maillet 1968, 187)

[72] *Man erlaube uns einigen poetischen Ausdruck, da überhaupt Prose wohl nicht hinreichen möchte. Ein ungeheurer Geist, wie er im Ozean sich wohl als Walfisch darthun konnte, stürzt sich in ein sumpfig-kiesiges Ufer einer heissen Zone; er verliert die Vorteile des Fisches, ihm fehlt ein tragendes Element, das dem schwersten Körper leichte Beweglichkeit durch die mindesten Organe verleiht. Ungeheuere Hilfsglieder bilden sich heran, einen ungeheueren Körper zu tragen. Das seltsame Wesen fühlt sich halb der Erde, halb dem Wasser angehörig und vermisst alle Bequemlichkeit, die beide ihren entschiedenen Bewohnern zugestehen.* (Goethe 1954 (1821), I, vol. 9, 247-248)

While the similarities between de Maillet's and Goethe's text are striking,[73] the difference of the scenarios concerns mainly the relatedness of the organisms: by Goethe the evolutionary change implies two mammals (although Goethe mistakenly called the cetacean a "fish"); in de Maillet's scenario a fish is transformed in a bird.[74] Is the strong similarity between both passages merely coincidental? Given the ample dissemination of de Maillet's ideas, Goethe might have adopted the evolutionary scenario from other contemporaneous authors influenced by the Mailletian system or even have developed his idea independently. However, it is not only the striking similarity of ideas that speaks for the hypothesis that Goethe borrowed de Maillet's idea. As Kohlbrugge (1912, 50) noted, Goethe lent *Telliamed* 1806[75] and again 1816 from a library in Weimar. On the other hand, Goethe mentioned de Maillet's ideas in other parts of his publications (Kohlbrugge 1912, 507; Neubert 1920, 18).

An example of transformist ideas close to the de Mailletian system can be found in Robert Chambers' *Vestiges of the Natural History of Creation* (first published anonymously in 1844).[76] In several parts of this work he implied a view on land forms originating from secondary aquatic organisms. This erroneous concept is compatible with Chamber's attempts to explain organismic evolution as a phenomenon of continuous, gradual, progressive and predictable steps. (As a deist, Chambers believed that God had created the laws of nature, without any intervention towards subsequent developments.) For instance, several passages of *Vestiges* imply that the land once seemed to be an invitation to create higher forms of life. It seems that the idea of animals abandoning terra firma (where, according to the concept of progressive transformism, they could "develop further") to return into the water was rather sophisticated and counterintuitive in this time. Chambers was not able to identify the erroneous views on aquatic discrepant organisms. He saw for instance the semi-aquatic platypus as belonging "to a class at the bottom of the mammalian" (Chambers 1844, 195), referring not only to the fact that this mammal lays eggs, but also to aquatic features which confused other early naturalists (see Appendix A), like the webbed feet and rubbery snout.

[73] Both authors envisaged (a) the transformation of an aquatic to a terrestrial organism; mentioned (b) an aquatic animal falling / being flushed on the shore; mentioned (c) organs used for propulsion in the aquatic environment as starting point for the subsequent development of organs of locomotion in a non-aquatic environment; envisaged (d) a scenario conveying the impression of a rather punctual or abrupt evolutionary change.

[74] Interestingly, as de Maillet and Lamarck, Goethe did not realize that the whale is a secondary aquatic mammal, and therefore inaccurate to exemplify such a transition. This topic will be treated in the next section.

[75] On 25 October of the same year Goethe mentioned *Telliamed* succinctly in one of his diaries: "Elpenor und die Fischerin. Telliamed. Hauptmann Gautier, Zeichner, zu Tische. Unterhaltung über den Krieg, die Kunst und die politischen Lagen. Abends bey Hofe. Geheimerath von Wangenheim von Eisenach" (Goethe 1805, 185).

[76] On Chambers' transformism possibly influenced by the Copernican revolution see footnote 39.

Chambers did not quote de Maillet, and although he discussed the Lamarckian system (Chambers 1844, 230-231), it is not possible to assess if Chambers took the concept of secondary aquatic animals descending from primary aquatic organisms from Lamarck's *Philosophie zoologique*. As already stated, the idea of terrestrial animals which moved "back into the water" was not an intuitive one, and naive assumption of gradual and progressive evolution were prone to produce concepts of platypus or dolphins as primary aquatic animals. Even today, educated non-biologists are often not able to discern clearly secondary from primary aquatic organisms. [77]

B.4 Discrepant evaluations of *Telliamed*

B.4.1 Darwin's historical sketch

In response to criticism[78] that he had not sufficiently considered early proponents of evolutionary ideas (Freeman 1977, 78), Darwin reviewed the topic in a historical sketch added to the 3th edition of his *Origin*[79] (see below). In the 6th and usually regarded as the last edition of *Origin*, he mentioned a total of 34 authors who accepted the modification of species (Darwin 1872, xii-xxi). The oldest evolutionary ideas pioneers he mentioned in this edition

[77] An interesting example can be found in the book *Sea Enchantress: The Tale of the Mermaid and her Kin.* In a passage which was probably hastily added shortly before the publication of the book, the authors wrote: "An eminent zoologist, Sir Alister Hardy, has recently propounded the theory that Ape-man, our ancestor, was obliged at one time to return to the sea to find his food. He may have left some of his kin the sea" (Benwell & Waugh 1961, 276). Although the authors were aware that Hardy argued towards an ape "returning" to the sea, they listed following argument for the aquatic scenario: "Even today man retains evidence of his marine ancestry. The human race still has faint traces of gills, and in a few cases these traces may be so marked as to warrant surgical removal" (Benwell & Waugh 1961, 276-277). Humans to not have vestigial gills - the authors probably refer to branchial cleft and arch anomalies (Waldhausen 2006). In any case, "vestigial gills" are misplaced in a discussion on a possible semi-aquatic scenario in human evolution as well as in a discussion on semi-aquatic mammals which descended from terrestrial species. See also Buffon's experiments in an attempt to bread an amphibious race of dogs (below, chapter B.4.3) and Steinmann's speculations on ichthyosaurs as ancestors of dolphins in Appendix D.

[78] In a review published in the Edinburgh Review, Owen (1860) wrote:

> Mr. Darwin rarely refers to the writings of his predecessors, from whom, rather than from the phenomena of the distribution of the inhabitants of South America, he might be supposed to have derived his ideas as to the origin of species. When he does allude to them, their expositions on the subject are inadequately represented. Every one studying the pages of Lamarck's original chapters (iii. vi. vii., vol. I., and the supplemental chapter of 'additions' to vol. ii. Of the '*Philosophie Zoologique*'), will see how much weight he gives to inherent constitutional adaptability, to hereditary influences, and to the operation of long lapses of time on successive generations, in the course of transmuting a species. The common notion of Lamarck's philosophy, drawn from the tirades which a too figurative style of illustrating the reciprocal influence of innate tendencies and outward influences have drawn upon the blind philosopher, is incorrect and unjust.

The passage is available online in *The Victorian Web* (http://www.victorianweb.org/science/science_texts/owen_review_of_origin.html#sixteen, accessed on 26 December 2013); in the same review Owen mentioned several times de Maillet as a precursor of Darwin's evolutionary ideas.

[79] This sketch is absent in the first two English editions of Darwin's *Origin* published in November 1859 and October 1860.

were Aristotle, his grandfather Erasmus Darwin (1731-1802), the French naturalist G. Leclerc de Buffon (1707-1788), Jean Baptiste de Lamarck (1744-1829), Étienne Geoffroy Saint-Hilaire (1772-1844), Lorenz Oken (1779-1851) and Johann Wolfgang von Goethe (1749-1832).

As pointed out by Egerton (1976, 453), the historical sketch was "a literature review and not a brief intellectual autobiography". As we will see, the historical sketch sheds light on problems Darwin faced in his attempts to separate his own views from earlier discredited ideas on evolution; the difficulty of this task is certainly one of the main reasons why he did not write such a review in the first edition of *Origin*.

It is interesting to see that the historical sketch is not in line with the above mentioned research by Mornet (see chapter B.3), who indicated that *Telliamed* in the 18th century was a "popular" scientific book. It might come to a surprise for some Darwin and de Maillet scholars that Darwin knew *Telliamed*, mentioning it in two *Origin's* editions that are rarely considered in historical investigations.

Although *Telliamed* was not a part of Darwin's Library, at least not at the time of his death[80], Darwin possessed a copy of it. In fact, the question of whether Darwin had a copy of *Telliamed* or not is hardly considered in the literature. The only concrete indication I had when I wrote on this topic (Bender 1999b, 59) was from Jordan, who pointed out that Darwin had known *Telliamed*, "because the same one copy stood in the *Catalogue of the library of Charles Darwin now in the botany at Cambridge* (Cambr. 1908) in his library" (Jordan 1914, 5, my translation). In the 1990s I did not have access to this catalogue; now it is published online.[81] According to this catalogue, Darwin had a copy of the *Telliamed* edition published in London in 1750 (Rutherford 1908, 54). The information on the background of this copy can be found in the correspondence Darwin had with the Scottish horticulturalist Isaac Anderson-Henry. In a letter to Darwin on 20 May 1867 Anderson-Henry asked if Darwin knew *Telliamed*, offering to send him an English translation of it dated 1750. He wrote: "Have you ever seen a singular book I fell in with lately the '*Telliamed*' of M. Maillet in which he treats 'of the origin of men & Animals'. My copy, a Translation, is dated 1750 [.] If you have not

[80] This information was confirmed by David Kohn (personal communication), the Director of the Darwin Manuscripts Project at AMNH. He referred to the comprehensive Bibliography that forms part of Charles Darwin's Library, which was produced by the Darwin Manuscripts Project and now appears on the BHL site.
[81] In (http://darwin-online.org.uk/content/frameset?itemID=A4&viewtype=text&pageseq=1 The Complete Works of Charles Darwin Online).

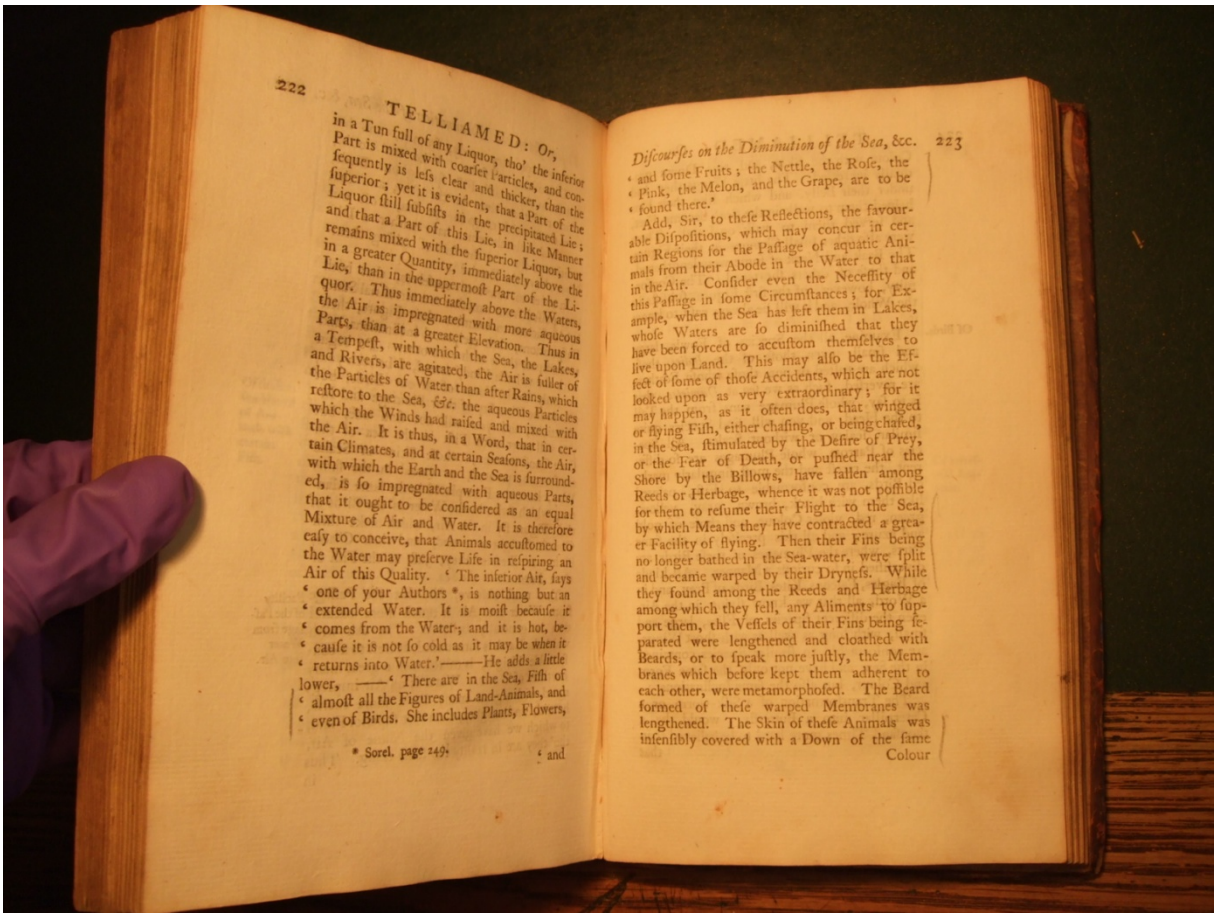
seen, and should wish to see it, I will gladly send it. It stoutly asserts the fact of men having *tails* & gives instances".[82]

Darwin answered on 22 May 1867: "You are so kind as to offer to lend me Maillet's work, which I have often heard of, but never seen. I should like to have a look at it, and would return it to you in a short time. I am bound to read it, as my former friend and present bitter enemy Owen generally ranks me and Maillet as a pair of equal fools" (Darwin 1903, 280).

I do not have confirmed information on how this copy came to Darwin, where it was stored and when it was rediscovered.[83] According to Annie Kemkaran-Smith, curator at the National Collections Group, English Heritage, the copy is now at Down House. It is listed as belonging to Cambridge University Library and is on loan together with other books from Darwin's library (pers. comm.); she kindly provided pictures showing Darwin's marginalia in this copy (see Fig. B.1). It is interesting to see that Darwin was interested in the parts of the work which also are mostly treated in detail here[84]; they are: (a) terrestrial animals having counterparts in the sea (De Maillet 1750, 222-223); (b) fishes crawling at the bottom of the sea as ancestors of terrestrial animals and flying fishes as ancestors of birds[85]; (c) flying fish transformed into a bird (De Maillet 1750, 223-224); (d) a sentence on the moons of the planets[86]; (e) terrestrial fruits having counterparts in the sea[87]; (f) the passage where de Maillet tries to explain some difficulties of his system concerning the evolution of organisms[88]; (g) human skin similar to the fish scales (De Maillet 1750, 258); (h) the sea as the cradle of all living organisms (De Maillet 1750, 259); (i) on several species of sea-apes, which are "precisely the same figure with those of the land" (De Maillet 1750, 225); (j) on "sea-bears" (De Maillet 1750, 226); (k)

[82] In *Darwin Correspondence Database*, http://www.darwinproject.ac.uk/entry-5542 accessed on 25 December 2013.
[83] The only information was given by Stott (2013, 129), who wrote that Anderson-Henry posted this copy to Kent in 1867, and that it disappeared into a box stored in the family attic at Down House; it was retrieved only in 1993. Unfortunately she did not give references to this specific source.
[84] I received the pictures only after the main text of the present analysis was finalized.
[85] On this page there is a typo: the page number is given as 122, instead of 221; Darwin corrected it (De Maillet 1750, 122 (sic: 221)).
[86] He marked the word 'Mars' in the sentence beginning with "If then as the Earth" (De Maillet 1750, 209).
[87] The passage marked begins with "They there find" until the end of the paragraph (De Maillet 1750, 219); he wrote at the margin "see pp 222,23", which refers to the passage on counterparts land/aquatic animals.
[88] Passage verbatim: „I am now to convince you, that without the Help of this new Creation, all the Species which now live in the Globe might have been there naturally produced, tho' they had been extinguished" (De Maillet 1750, 276).

on men with tails found in several countries of the world[89]; (l) on humans interbreeding with apes and having descendants able to speak (De Maillet 1750, 273).


222 TELLIAMED: Or,

in a Tun full of any Liquor, tho' the inferior Part is mixed with coarser Particles, and consequently is less clear and thicker, than the superior; yet it is evident, that a Part of the Liquor still subsists in the precipitated Lie; and that a Part of this Lie, in like Manner remains mixed with the superior Liquor, but in a greater Quantity, immediately above the Lie, than in the uppermost Part of the Liquor. Thus immediately above the Waters, the Air is impregnated with more aqueous Parts, than at a greater Elevation. Thus in a Tempest, with which the Sea, the Lakes, and Rivers, are agitated, the Air is fuller of the Particles of Water than after Rains, which restore to the Sea, &c. the aqueous Particles which the Winds had raised and mixed with the Air. It is thus, in a Word, that in certain Climates, and at certain Seasons, the Air, with which the Earth and the Sea is surrounded, is so impregnated with aqueous Parts, that it ought to be considered as an equal Mixture of Air and Water. It is therefore easy to conceive, that Animals accustomed to the Water may preserve Life in respiring an Air of this Quality. 'The inferior Air, says 'one of your Authors *, is nothing but an 'extended Water. It is moist because it 'comes from the Water; and it is hot, be-'cause it is not so cold as it may be when it 'returns into Water.'——He adds a little lower, ——'There are in the Sea, Fish of 'almost all the Figures of Land-Animals, and 'even of Birds. She includes Plants, Flowers,

* Sorel. page 249. 'and

Discourses on the Diminution of the Sea, &c. 223

'and some Fruits; the Nettle, the Rose, the 'Pink, the Melon, and the Grape, are to be 'found there.'

Add, Sir, to these Reflections, the favourable Dispositions, which may concur in certain Regions for the Passage of aquatic Animals from their Abode in the Water to that in the Air. Consider even the Necessity of this Passage in some Circumstances; for Example, when the Sea has left them in Lakes, whose Waters are so diminished that they have been forced to accustom themselves to live upon Land. This may also be the Effect of some of those Accidents, which are not looked upon as very extraordinary; for it may happen, as it often does, that winged or flying Fish, either chasing, or being chased, in the Sea, stimulated by the Desire of Prey, or the Fear of Death, or pushed near the Shore by the Billows, have fallen among Reeds or Herbage, whence it was not possible for them to resume their Flight to the Sea, by which Means they have contracted a greater Facility of flying. Then their Fins being no longer bathed in the Sea-water, were split and became warped by their Dryness. While they found among the Reeds and Herbage among which they fell, any Aliments to support them, the Vessels of their Fins being separated were lengthened and cloathed with Beards, or to speak more justly, the Membranes which before kept them adherent to each other, were metamorphosed. The Beard formed of these warped Membranes was lengthened. The Skin of these Animals was insensibly covered with a Down of the same Colour

Figure B.1 Picture of Darwin's copy of *Telliamed* showing lines placed to mark up passages he was especially interested in. It is not surprising that he marked de Maillet's sentences on terrestrial organisms having counterparts in water and the famous passage of a fish transformed into a bird. Photography by Annie Kemkaran-Smith.

Although the historical sketch was prepared for the first authorized American edition published in May 1860, curiously it first appeared in the first German edition translated by Heinrich Georg Bronn from the second English edition and published in April 1860.[90] This German historical sketch was shorter compared to the third English edition[91] of March 1861. Darwin mentioned in it that, apart from the writers of the classical period and of de Maillet and Buffon (with whose writings he stated not to be familiar), Lamarck's opinion on species

[89] Darwin wrote "Men with Tails" beside this passage (De Maillet 1750, 247). As we will see below, Owen (1860) used exactly this sentence to compare with Darwin's views on bears as precursors of whales to make Darwin appear ridiculous.

[90] See Johnson (2007) for an analysis of Darwin's historical sketch; see also Darwin (1993, vol. 8, 572).

[91] The title was almost the same as in the sixth edition of 1872, which is usually regarded as the last: "An historical sketch on the progress of opinion of the origin of species" -, but without the subtitle "Previously to the publication of the first edition", which appears from the sixth edition onwards.

change was the first that, "excited much attention" (*Aufsehen erregte*).[92] The text in English, when finally published, appeared in July 1860 in the fourth printing of *Origin* in the United States under the title "Preface", followed by "Contributed by the author to this American Edition".[93] In this edition Darwin wrote: "Passing over authors of the classical period, and likewise Demaillet and Buffon, with whose writings I am not familiar, Lamarck was the first man, whose view that species undergo change excited much attention" (Darwin 1860a, v).

As far as I know, de Maillet is not mentioned in any of the English editions of *Origin*, and most reprints[94] do not refer to this specific difference in the historical sketches. In the fourth English edition of 1866 (p. xiii), Darwin added a footnote on Aristotle to the sentence "Passing over allusions to the subject in the classical writers"; this footnote was also reproduced in subsequent editions (Darwin 1872, xii; Darwin 1876a, xv).

There is also an indirect, early link to *Telliamed*. Darwin wrote in Notebook B178e from 1838[95] a passage where *Telliamed* is mentioned; the passage is almost a verbatim quotation of following statement published in the *Bulletin de la société géologique de France* (1re série, Tome IV) from the Société géologique de France, 1834 (pp. 90-110), reporting on the meeting of 2nd December 1833. In this statement, Deshayes criticized Geoffroy Saint-Hilaire for referring to Lamarck's rudimentary transformist ideas in *Hydrogéologie* instead of referring to the more elaborated ideas expressed in *Philosophie zoologique* and in the introduction of his *Histoire des animaux sans vertèbres* (Lamarck 1815-1822, 7 vol.).[96] In Deshayes' opinion,

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[92] The passage reads as follows: „*Abgesehen von den Schriftstellern der klassischen Periode, so wie von Demaillet und Buffon, mit deren Schriften ich nicht vertraut bin, war Lamarck der erste, dessen Meinung, dass Arten sich verändern, Aufsehen erregte*" (Darwin 1860c, 1). Already the second German edition was based on the third English edition and does not mention de Maillet (Darwin 1863).

[93] It is the work number 380 in Freeman's list of Darwin's works (Freeman 1977, 85), with "*new edition, revised and augmented by the author"* on the title page.

[94] See below. The variorum text of *Origin* edited by Morse Peckham (Darwin 1959) does not belong to the exceptions, since it does not consider the American editions.

[95] In http://darwin.amnh.org/viewer.php?eid=77099 Darwin Manuscripts Project.

[96] The original in French reads as follows:

> M. Deshayes, répondant à ce que M. Geoffroy Saint-Hilaire a exposé dans la séance précédente en présentant son opuscule intitulé : Paléontographie, réclame en faveur de notre célèbre Lamarck la priorité de cette idée, que les animaux sont modifiés dans leur organisation par les circonstances ambiantes. « Cette thèse, dit-il, a été développée par Lamarck, non seulement dans sa philosophie zoologique, en 1809, mais encore dans sa belle introduction à l'histoire des animaux sans vertèbres, 1815. « M. Deshayes fait observer qu'il n'est pas juste de citer, comme l'a fait M. Geoffroy Saint-Hilaire, l'Hydrogéologie de Lamarck, ouvrage antérieur aux deux précédents, et dans lequel cette idée n'est exposée que très accessoirement[.] (p. 99)

I quoted the passage from the digital version available in http://fr.wikisource.org/wiki/Bulletin_de_la_soci%C3%A9t%C3%A9_g%C3%A9ologique_de_France/1re_s%C3%A9rie/Tome_IV/S%C3%A9ance_du_2_d%C3%A9cembre_1833 (accessed on 11 January 2014). I wish to thank David Kohn, Director of the Darwin Manuscripts Project at AMNH, who drew my attention to the reference concerning *Telliamed* in Darwin's notebook.

Lamarck did not share the ideas expressed in *Telliamed*, which were also reproduced by Bonnet and Rodig, as Saint-Hilaire seemed to believe.[97]

As seen from Darwin's notice in Notebook B178e, Darwin was already aware of statements on *Telliamed* as a book defending transformist ideas as early as 1838. Interestingly, this diary entry was written shortly after what is often regarded as the period in which he changed his belief concerning the fixity of species, around the end of 1836 (Limoges 1970b, 9). See also below (chapter B.4.3), where Cuvier mentioned Robinet, Rodig and Lamarck as amendments to de Maillet's transformism.

The reason for omission of de Maillet's name in later versions of the historical sketch is insightful for understanding the problems Darwin and later evolutionists had to face when discussing the ideas of an 18th century precursor of evolutionism who believed that humans descended from *hommes marins*. Darwin realized that mentioning Buffon and de Maillet in connection with "allusions to the subject" was not precise – this sentence is only true concerning Buffon. Darwin had to make a decision – he would have to treat *Telliamed* separately or to erase de Maillet's name to correct the issue that arose from the expression "allusion". The first alternative was associated with three problems. First, de Maillet defended views which were obviously perceived as extremely speculative; second, it was impossible to refer to *Telliamed* as a work mentioning evolutionary ideas marginally; finally, as shown below, the book had been praised by his friends, Charles Lyell and Thomas Huxley. The danger of Darwin's evolutionary system being associated with a speculative author became evident after the publication of a review in the *Edinburgh Review* where Owen associates Darwin's famous bear / whale statements with de Maillet's flying-fish / bird views (see below chapter B.4.3). This review certainly played the most important part in Darwin's decision to delete de Maillet's name from the historical sketch. We see in the third English edition Darwin wrote: "Passing over authors from the classical period to that of Buffon, with whose writings I am not familiar, Lamarck was the first man whose conclusions on this subject excited much attention" (Darwin 1861, xiii).

[97] The original passage reads as follows:

> [...] enfin, M. Deshayes termine en affirmant de la manière la plus positive, et en citant les pages 129 et 130 de l'introduction précitée, que jamais Lamarck n'a partagé les idées systématiques de Telliamed, reproduites par Bonnet et Rœdig [Rodig], comme paraît le croire M. Geoffroy Saint-Hilaire. (pp. 99-100)

In:
http://fr.wikisource.org/wiki/Bulletin_de_la_soci%C3%A9t%C3%A9_g%C3%A9ologique_de_France/1re_s%C3%A9rie/Tome_IV/S%C3%A9ance_du_2_d%C3%A9cembre_1833, accessed on 11 January 2014.

This solution was still not optimal, as Darwin was aware that the above statement implied an astonishing gap in his historical knowledge. This applied to not only Buffon's works, which could be easily forgiven, but at the same time gave credence to the possibility of identifying Buffon as an important forerunner of evolutionary ideas. More serious was probably the section on authors of the classic period, since Darwin would certainly not like to be regarded as insufficiently educated relative to the intellectual heritage of ancient thinkers. So the statement was again modified in the 5th edition of 1869. He mentioned Aristotle as an example of a classical writer and included at least a negative aspect related to Buffon's evolutionary views:

> Passing over allusions to the subject in the classical writers,* [footnote on Aristotle] the first author who in modern times has treated it in a scientific spirit was Buffon. But as his opinions fluctuated greatly at different periods, and as he does not enter on the causes or means of the transformation of species, I need not here enter on details" (Darwin 1869, xv).

It seems that most investigators in the past were not aware of the specifics concerning De Maillet in the first German edition or the fourth American printing from 1860. Despite the enormous work that has been carried out on Darwin, even today's historians (apart from the few specialists mentioned above) ignore this difference, as explained by Johnson, who investigated the history of the historical sketch (although he did not specially focus on de Maillet):

> Most accessible editions of the Origin are reprints of the sixth English edition (or translations thereof) and so, unlike the first English edition, include the "Historical Sketch" as it appeared in the sixth English edition. The bibliographic details of the various editions of Darwin's Origin are no doubt of subordinate interest to the general reader, but in view of the numerous changes Darwin made to successive editions it behoves those working in Darwin studies to be attentive to these subtleties. (Johnson 2007, 529)

My own copies of German editions of *Origin* endorsed Johnson's judgement (Darwin 1876b; Darwin 1892; Darwin 1899; Darwin 1989; Darwin 1990); furthermore, from the 26 editions of *Origin* published in *Darwin Online* which I can read[98] only the first German edition mentioned de Maillet in the historical sketch. In fact, I myself did not have the opportunity to consult the fourth American printing from the original until shortly before submission of this thesis (on 14 February 2014); I quoted therefore from the historical sketch fully reproduced in

[98] In http://darwin-online.org.uk/contents.html, accessed at 22 December 2013. I could not check the Russian edition.

Darwin (1993, vol. 8, 572-573) which I compared to the only online version available, which is however without OCR correction.[99] Please note that the excellent variorum text of *Origin* edited by Morse Peckham (Darwin 1959) does not contain the changes in the historical sketch from the American editions (or other non-English editions). In the meantime, after I pointed out the absence of the 4th American printing in Darwin Online, John van Wyhe, Senior Lecturer at Darwin Online, added it to the website.[100]

In the sixth English edition and subsequent reprints and translations thereof, de Maillet is implied as an author not belonging to the category of scholars who had treated evolutionism "it in a scientific spirit". By passing over de Maillet in the historical sketch, Darwin did not acknowledge the enormous impact of de Maillet's evolutionary ideas in the development of the evolutionary view. Darwin cannot be blamed for his decision on de Maillet, as the association between *Origin* and *Telliamed* would certainly instigate similar attempts to undermine Darwin's ideas (see below, chapter B.4.3). However, the sketch had (and still has) a significant impact on biologists who consulted *Origin* to use Darwin's views on what he believed to be the precursors of his own evolutionary system, and the absence of de Maillet in this review certainly had a sensible impact in later historical analyses.[101]

B.4.2 The underrepresentation of de Maillet's ideas in textbooks

Before we begin to analyse the reception of *Telliamed*, it is useful to address the question of how often de Maillet is mentioned as a precursor of evolutionary ideas in modern biological textbooks. Eiseley, after discussing Telliamed, was surprised to note that this work was rather ignored in textbooks of his own library; "Telliamed, though known to English historians of science, has passed comparatively unnoticed. Of five histories of biology which I have

[99] In http://www.archive.org/stream/onoriginspecies01unkngoog/onoriginspecies01unkngoog_djvu.txt, accessed on 22 December 2013. OCR: Optical Character Recognition.

[100] In http://darwin-online.org.uk/content/frameset?itemID=F380&viewtype=text&pageseq=1, accessed on 15 February 2014. I wish to thank John van Wyhe for his efforts.

[101] See Samuel Butler's book *Evolution, old and new, or, The theories of Buffon, Dr. Erasmus Darwin and Lamarck, as compared with that of Charles Darwin* in an early example of historical investigation closely oriented to the historical sketch (Butler 1879). It is probably not wrong to assume that most early and modern historians expressing detailed views on the roots of the evolutionary ideas after 1860 consulted Darwin's historical sketch in the course of their investigations. Summarized reviews on the history of evolutionary thought on the World Wide Web seem to endorse the result of our review on biological textbooks in not mentioning de Maillet. For instance, from the 20 first results of a Google search ("history of evolutionary thought") carried out on 26 December 2013, the summaries of the history of evolutionary thought do not mention de Maillet, with one remarkable exception - the article in *Wikipedia* written in English (http://en.wikipedia.org/wiki/History_of_evolutionary_thought, accessed on 26 December 2013). Interestingly, the corresponding articles in German, Italian, Portuguese, Spanish, Romanian, Dutch, Catalan and even French (!) follow again the general trend of not mentioning de Maillet. Also the article "History of evolutionary thought" in EvoWiki, which lists a "timeline of important events in evolutionary biology", does not mention de Maillet (http://evolutionwiki.org/wiki/History_of_evolutionary_thought, accessed on 26 December 2013).

consulted on my shelves, only one mentions Telliamed - and then only in a passing sentence" (Eiseley 1961, 30).

To compare Eiseley's observation with works published after 1958, I checked 27 randomly chosen[102] biological introductory books for undergraduate and postgraduate students or books on evolution written by experts for general readers published between 1960 and 2013 for text on the development of evolutionary thoughts (see Table B.1). The sample contains textbooks on biology, evolution, species concept, palaeontology, botany and zoology published in English, German and Italian; two of the works are books on evolution written by experts for general readers (Mayr 2001; Norman 1994). I did not consider here the specialized literature on history of science, as they will be treated separately, but only textbooks, where, for space constraints, the precursors of the evolutionary idea are only succinctly mentioned. Authors were not listed in the table when they did not play a significant role in the scientific discussion (for instance Robert Fitzroy). The same applies to authors mentioned within detailed discussions on a specific topic, for instance, concerning species concept (e.g., Willmann 1985) or the development of palaeontology (e.g., Ziegler 1986). Authors included in these chapters are regarded as major figures whose contributions had a positive or negative influence on the consolidation of evolutionary concepts. Authors sporadically or consequently coined as proponents of evolutionary ideas are underlined. The number of books indicates how many books mentioned a specific author.

Statements on the history of evolutionary views from textbooks are insightful because, due to space constraints, these works can consider only a limited spectrum of ideas expressed by other scientists. In doing so, they help to retell both accurate and inaccurate aspects of the history of a certain field. Although the sample of this investigation is small, it is useful to give at least an approximate picture of common misconceptions or omissions concerning modern views on the history of evolutionary ideas.

[102] Inspired by Eiseley, 15 of the books were randomly chosen from my personal library. In order to enlarge the number of reference works, seven other titles have been added from the open access library of the University of Bern. The only criteria for the inclusion in the sample were the presence of a historical sketch and publication year (after 1958).

Table B.1. Authors mentioned in chapters summarizing the development of evolutionary ideas in 27 randomly chosen textbooks[103] published in English, German and Italian between 1960 and 2013

Authors	Number of books
Charles Darwin	27
B. de Lamarck	26
Charles Lyell, George Cuvier	15
Alfred R. Wallace	14
Carl Linnaeus	12
Thomas R. Malthus	9
G. Leclerc de Buffon	8
Aristotle	7
Ernst Haeckel	5
James Hutton, Geoffroy Saint-Hilaire, Plato	4
Anaximander, Gregor Mendel, John Henslow, Immanuel Kant, Robert H. Hooke, Robert Chambers, Pierre L. Maupertuis, Denis Diderot, Erasmus Darwin, John Ray	2
Herbert Spencer, Johannes Müller, Alexander Pope, Empedocles, Svante Arrhenius, Julien O. de La Mettrie, August Weismann, Johann W. von Goethe, G. R. Treviranus, Pliny, J.C.M. Reinecke, H.G.Bronn, Charles Bonnet, Benoît de Maillet, Richard Owen	1

In the above review, de Maillet was mentioned by only one author. It is certainly not a coincidence that this (positive) reference to de Maillet by Bernhard Ziegler (1986, 2) is found in a historical sketch on the development of *geological* and *palaeontological* research. As we will see below, *Telliamed* is often considered as a landmark in the history of these fields by

[103] (Autorenkollektiv 1992, 855; Autorenkollektiv 2002, 386; Belk & Maier 2013, 224-227; Bickel et al. 2001, 341-347; Campbell & Reece 2006, 504-507; Creager et al. 1986, 132-136; Frisch 1960, 168-198; Futuyma 1998, 17-21; Hoefnagels 2013, 220-221; Kühn 1972, 434; Kutschera 2008, 24-31; Linder et al. 1961, 278-280; Linder & Bayrhuber 1992, 421-425; Mader & Windelspecht 2013, 272-274; Mayr 2001, 5-11; Norman 1994, 18; Oram 1982, 277-283; Purves et al. 2006, 4-5; Raven et al. 2006, 227-229; Reece 2011, 499-503; Ridley 1993, 7-11; Starr 2013, 237-243; Strickberger 2000, 30; Wehner & Gehring 1990, 540-543; Willmann 1985, 33-39; Ziegler 1980, 2-3; Zrzavý et al. 2009, 6-7, 10).

specialized historians; this trend is even more evident after the publication of Carozzi's edition of this work. Carozzi himself specialized in the history of geology.

In the opinion presented here, the under-representation in textbooks does not reflect basic historical facts on de Maillet. This statement does not imply a criticism of the textbooks quoted above, as their historical sketches reflect scholarly consensus. In fact, the misconceptions about the role that de Maillet played in the biological sciences were not created by modern historians, but adopted from biased historical analyses of late 19th and early 20th century.

B.4.3 Main points raised by early and modern authors in their negative evaluations of de Maillet's evolutionary ideas

Darwin's historical overview was the beginning of an extensive line of research[104] in the history of biology.[105] Especially the earlier phase of this research program was, however, anything but objective. In the decades around 1900, an intensive debate about the validity of "Darwinism" was in progress (Bowler 1983). Anti-Darwinian historians sometimes used their analysis to disdain Darwin's achievements. An extreme example of this is Kohlbrugge's article *War Darwin ein originelles Genie*? (Was Darwin an original genius?) (Kohlbrugge 1915), in which 57 pre-Darwinian proponents of evolutionary ideas are listed to expose Darwin's priority-claims as exaggerated.[106]

The study of the history of evolutionary theory has gained much distance and objectivity since the elimination of fundamental conflicts between different areas of biology in the 1930s and

[104] In an early phase, 189 single naturalists reviewed succinctly the ideas of authors from the 18th and early 19th century proposing "*transformation des espèces*", to use the expression of Cuvier (1841, 79) when he discussed de Maillet's evolutionary views (see full quotation below).

[105] Several works were published on the history of evolutionary thinking, so that only a very frugal selection of the works can be listed here (for historical investigations focusing on the history of anthropology see Appendix D). The author consulted investigations written originally or translated into German (Engels 1995; Junker 1998a; Kohlbrugge 1914; Kohlbrugge 1912; Kohlbrugge 1915; Krause 1879; Krause 1880; Lang 1877; Lefèvre 1984; Potonié 1890; Rádl 1909; Schindewolf 1941; Todes 1995; Uhlmann 1923; Wenzel 1982; Young 1993; Zimmermann 1953), in French (Bourdier 1960; Lanessan 1914; Quatrefages 1870) and in English (Bowler 1975a; Bowler 1973; Bowler 1989; Burckardt 1983; Burckhardt, Jr. 1977; Burkhardt, Jr. 1972; Butler 1879; Coleman 1964; Crocker 1959; Eiseley 1961; Farber 1999; Friedman & Diggle 2011; Ghiselin 2003; Gillispie 1959; Glass 1959a; Glass 1959b; Glass 1959c; Greene 1961; Haber 1959b; Haber 1959c; Larson 2004; Lovejoy 1959a; Lovejoy 1959b; Lovejoy 1959c; Lovejoy 1959d; Lovejoy 1959e; Mayr 1982; Oppenheimer 1959; Osborn 1924; Richards 1982; Ruse 1981; Ruse 1993; Sapp 2003; Secord 2000; Temkin 1959; Wells 1973; Zirkle 1941; Zirkle 1946; Zirkle 1954).

[106] In this article, which is provided through and through with ironic and derogatory remarks about Darwin, Kohlbrugge described Darwin's historical sketch as „extremely superficial" (*äusserst oberflächlich*), an utmost unfair assessment when it is considered that Darwin's historical sketch represents the first-ever attempt to present the history of evolutionary theory. It seems that Kohlbrugge forgot that he published his own investigation on the topic in 1915 (54 years after Darwin published his own historical studies) and that he had, unlike Darwin, access to secondary literature on this topic - Darwin's historical sketch was one of them.

1940s and the formulation of the synthetic theory of evolution. Although new avenues for a more realistic analysis of the emergence of evolutionary thinking have been opened up, de Maillet's evolutionary ideas are – as we will see below – often negatively evaluated both by biologists as well as historians. (This judgment is not shared by all naturalists in the 19th century and early 20th century and modern historians; see below, chapter B.4.3) The results of an analysis of this evaluation are insightful and are taken up in later chapters of the present thesis. My most important conclusions are related to the following topics: On the one hand, early and modern views on de Maillet's ideas reveal crucial aspects of the attempts to establish the boundaries of scientific debate, a topic which is essential in our analysis of modern hypotheses on human evolution (see topic "aquatic hypotheses" in Appendix D). On the other hand, they will supply new insights related to the use of analogies in the emergence of evolutionary thinking in the 18th century.

De Maillet's views as fantasies, fancies, fiction, or threat to Christian dogma

In a book on shells released in 1752, only four years after the first publication of *Telliamed*, Dezallier d'Argenville wrote: "What a folly in this author to substitute Telliamed for Moses, to force man out of the depths of the sea, and for fear that we might descend from Adam, to give us marine monsters for ancestors! Only a kind of godless could invent such dreams." (Dezallier d'Argenville 1757, 74, my translation). [107] (A similar reaction can be found in lengthy and vociferous passages published in a German popular science magazine.)[108] The indignation at the possibility that humanity could have emerged from something other than Adam is comparable to the reactions towards Isaac La Peyrère's pre-Adamite views, first published in 1655,[109] as well as towards the implications of Darwin's *Origin.* Although Darwin conceived his main work in a way to avoid the topic on human evolution,[110] it was widely perceived as implying the idea that human originated from apes,[111] an assumption

[107] Quelle déraison à cet auteur, de substituer Telliamed à Moïse, de faire sortir l'homme du fond de la mer; et de peur que nous ne descendions d'Adam, de nous donner des monstres marins pour aïeux ! Il n'y a que des impies qui puissent inventer de pareilles rêveries.

[108] This specific volume of *Allgemeines Magazin der Natur, Kunst und Wissenschaften* was edited by the German astronomer Johann Daniel Titius (1729-1796). This journal was the source for important naturalists, as for example, Immanuel Kant (Kautzleben 2004, 126). The articles on de Maillet (Anonymous 1753a; Anonymous 1753b; Anonymous 1753c) were published only five years after the first edition of *Telliamed*. Some parts of the criticism imply that the work was known in Germany and Italy.

[109] On La Peyrère and his influence see Allen (1949, 86-91), Grayson (1983, 140-142) and Popkin (1987).

[110] It is usually stated that Darwin dared to make only one statement concerning human evolution in the first edition of *Origin* – "Light will be thrown on the origin of man and his history" (Darwin 1859, 488). However, this does not correspond to the facts, as Darwin touched the topic in several parts of *Origin* (Bajema 1988, 404); Bajema explains how Darwin also played a role in the dissemination of this myth.

[111] On the reception of Darwin's evolutionary ideas by general readers see Ellegård (1958, 293-331). Several works were published on the role of primates in the way that humans deal with the animal-human boundary

which certainly was not less shocking than de Maillet's explicit interpretation of human genesis.

This was not the only analogy between de Maillet and biblical figures, as we can see in following translated passage from Voltaire's *Dictionnaire philosophique* (first published in 1764), where he wrote:

> It is really strange that men, while denying a Creator, should have attributed to themselves the power of creating eels[112]. But it is yet more deplorable that natural philosophers, of better information, adopted the jesuit Needham's ridiculous system, and joined it to that of Maillet, who asserted that the ocean had formed the Alps and the Pyrenees, and that men were originally porpoises, whose forked tails changed in the course of time into thighs and legs. Such fancies are worthy to be placed with the eels formed by meal. (Voltaire 1824, 340)

In the case of Voltaire, the aggressive response was motivated by the perception of *Telliamed* as an attempt to mimic Christian doctrine, an interpretation which is endorsed by an even sharper criticism Voltaire expressed (hidden under the cover name of M. de Morza) in his books *Cabales:*

> This consul Maillet was one of those charlatans who wanted to imitate God, and create a world with words. It was he who, abusing the story of some changes that arrived in the world, claims that the seas had formed the mountains, and that fish have changed into men. So when this book was printed, one did not fail to dedicate it to Cyrano de Bergerac. (Voltaire 1772, 36-37, my translation)[113]

A similar statement can be found in his *Singularités de la nature*. In the chapter "De la formation des montagnes" he criticized de Maillet's and Buffon's views that mountains were formed by the effect of the seas over a long period of time. He wrote:

> What then is the true system? the one of the great Being who has made all, and who has given to each element, to each species, to each genus its form, its place, and its eternal functions. The Great Being who has formed the gold and iron, the trees, the plants, man, and the ant, has

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and on apes as "the missing link"(Barnard 1995; Barsanti 1990; Barsanti 1995; Blanckaert 1995; Cartmill 2001; Corbey 1995; Corbey 2005; Dougherty 1995; Haraway 1989; Janson 1952; Kjærgaard 2011; Kruk 1995; Morris & Morris 1966; Nash 1995; Reybrouck 2001; Wokler 1995).

[112] He refers to the English scientist and Catholic priest John Needham, who in middle of the 18th century tried to prove by experiments that microscopic creatures ("eels") can emerge from decaying organic substances (see Fellows 1970, 31).

[113] *Ce consul Maillet fut un de ces charlatans dont on a dit qu'ils voulaient imiter Dieu, et créer un monde avec la parole. C'est lui qui, abusant de l'histoire de quelques bouleversements avérés, arrivés dans ce globe, prétend que les mers avaient formé les montagnes, et que les poissons avaient été changés en hommes. Aussi quand on a imprimé son livre, on n'a pas manqué de le dédier à Cyrano de Bergerac.*

> made the ocean and the mountains. Men have not been fish, as Maillet says; all is probably what it is by immutable laws. I cannot repeat too often that we are not gods who can create a universe with a word.(Voltaire 1831, chapter XI, 241, translated by Francis C. Haber)

Voltaire stressed the most bizarre-sounding aspects of de Maillet's system, an invitation to consider the whole system as a product of wild fantasy – a strategy found in several early and modern succinct criticism of the biological ideas expressed in *Telliamed*.

The French geologist and palaeontologist Adolphe d'Archiac suggested putting aside the "fantastic part of his book" (*cette partie fantaisiste de son livre*) (D'Archiac 1864, vol. 1, 276). When taking into consideration the first four conversations, he believed that "*Telliamed* is better than its reputation" (D'Archiac 1864, vol. 1, 276, my translation). The positive[114] evaluation of de Maillet's geological views and contrasting it with his biological ideas is also popular in modern publications (see below).

It is understandable that several naturalists and theologians in the second half of the 18th century and the first half of the 19th century reacted with indignation when confronted with the different aspects of de Maillet's evolutionary idea; likewise it is also reasonable that these early critics focused on aspects of de Maillet's arguments, which they perceived as more vulnerable instead of considering the whole system. However, as I show below, a similar reaction can be found in commentaries of *Telliamed* published in the 20th and 21st century.

In his work on *scala nature*, Thienemann described *Telliamed* as a highly original book. However, he mentioned it mainly to show that the belief on "fabulous merman and mermaids" (*fabelhaften Meermänner und Meerweiber*) were still most abundant in works of the 18th century (Thienemann 1909, 227).

Similarly, the following statement by Osborn expressed both a positive and a negative evaluation of *Telliamed*:

> In these transformations De Maillet was not embarrassed by the fixity of characters or by the fact that no such metamorphoses had ever been witnessed. Yet, we find buried in all this fiction two suggestions of theory. De Maillet claims for the scientist the right to search into Nature direct for her secrets. He finds in the world proofs that the days of Genesis were great

[114] Although the geological aspects of *Telliamed* were often well received by early and modern naturalists, some early authors criticized de Maillet's views regarding the diminution of the sea. An interesting example is provided by the detailed examination by Nicolas Desmarest in his *Encyclopédie méthodique: géographie physique;* he disagrees with de Maillet's idea that the position of the coasts changed over time (Desmarest 1828, 319-327).

> epochs of time, and he suggests in his metamorphoses, absurd as they are, the idea of the modification of organisms by environment and habit, and the transmission of these modifications to the descendants; in other words, he advocates the 'transmission of acquired characters'" (Osborn 1924, 112-113)

Arnold Lang published in the journal *Kosmos* a paper with crude, one-sided and often incorrect remarks on de Maillet's ideas (Lang 1878). His criticism was revised promptly by Ernst Krause, editor of *Kosmos*, in a footnote at the end of Lang's paper. Krause rectified Lang's statements, indicating that Lang did not give de Maillet the recognition he deserved. He remembered that these were the first ideas on the evolution from simple to complex organisms ever expressed (Krause in Lang 1878, 261); see also Krause (1880, 107-109).

In a footnote in his book on history of biology, Erik Nordenskiöld characterized *Telliamed* as a "natural philosophical work" (*naturphilosophisches Werk*) in which the evolutionary phenomena were described "in the highest fantastic way" (*auf höchst phantastische Weise*) (Nordenskiöld 1926, 332). Similarly to D'Archiac (see above), Karl von Zittel regarded *Telliamed* as a very original and important work on geology, but referred to the two last chapters (which contain de Maillet's evolutionary arguments) as "unfounded fantasies" (*grundlose Träumereien*) (Zittel 1899, 44). Guyénot mentioned the evolutionary ideas by de Maillet and Buffon. He regarded the two works "of very unequal value" (*de valeur très inégale*), but recognized that they definitely disseminated ideas regarding the origin of fossils and sedimentary terrain (Guyénot 1941, 353); for him de Maillet's transformism "belongs in the realm of fables" (*du domaine de la fable*) (Guyénot 1941, 388), and concluded: "After the two fantastic precursors [Robinet and de Maillet], the work of Maupertuis seems more serious and profound"[115] (Guyénot 1941, 389, my translation). Gayon, a specialist on Charles Darwin, believes that it is useless to begin the account of evolutionary ideas before Darwin (Gayon 1999, 392), a similar sentiment as expressed by François Jacob (see below). King-Hele, after explaining that "Between 1740 and 1790 there were many, most notable perhaps Diderot, De Maillet and Goethe, who believed that species are variable" concluded that "their beliefs, like those of the ancient Greeks, cannot be regarded as more than intelligent speculation" (King-Hele 1963, 66); as Erasmus Darwin's biographer he concluded (perhaps not very surprisingly) that "The credit for first propounding a well-rounded theory of evolution, with examples in support, belongs instead to Erasmus Darwin" (King-Hele 1963, 67). The designation of de Maillet's biological views as "fantasies" is also often used in

[115] Après ces deux précurseurs fantaisistes, l'oeuvre de Maupertuis n'en paraît que plus sérieuse et plus profonde.

passages of modern works (Ferenbach 1982, 398; Glass 1959b, 81). These and other similar statements will not be further discussed here, as the criteria used for them cannot be assessed from these succinct texts.

Criteria for a classification of de Maillet's views as lacking any evolutionary concept

A criterion sporadically used in modern evaluations of de Maillet's evolutionary ideas is supplied by the French biologist François Jacob (1920 – 2013). He regarded de Maillet as non-evolutionist, because he only had the transition from water to land life in mind, a concept lacking organismic changes or increasing complexity (Jacob 1972, 150), a view sporadically adopted or independently formulated by other authors (see, e.g., Lefèvre 1984, 28). In fact, the transition of organisms from an aquatic to a terrestrial environment is central in de Maillet's system. The most quoted statement from *Telliamed* – the description of a flying-fish turning into a bird (see above, chapter B.3) – illustrates the importance de Maillet gave to this topic. The frequent quotation of this passage implies two criticisms: one, the lack of a solid concept of systematics in *Telliamed;* the other, the extent to which de Maillet believed that organisms are transformed through drastic (saltation) instead of gradual changes. Both criticisms are used as self-evident demonstration for the absence of a concept of evolutionary changes in *Telliamed*. As we will see later, the saltation argument stands in stark contradiction to the views expressed by several modern authors, who stress the concept of eternal recurrence implied in the Mailletian system. Another interesting aspect of the criticism is from a comparison with a similar evaluation proposed by Junker and Hossfeld (2001). They summarise de Maillet's views, stressing that this work is important as it documents the extent to which some writers of the 18th century were liberated from the limited thinking of earlier centuries. Concerning the similarities between the Mailletian ideas and today's evolutionism, they write:

> Despite the similarity that this transformation has to today's notion of the origin of terrestrial organisms, one cannot speak of a true theory of evolution. The emphasis of this system lies clearly on the phase of origin, of spontaneous generation, and the subsequent changes in various landforms that correspond more to the metamorphosis[116] of an individual. (Junker & Hossfeld 2001, 38, my translation)

[116] With this expression, the authors pointed out an important aspect of de Maillet's biological ideas – the similarity with the idea of ontogeny, an element which might be interpreted as de Maillet's close interpretation of Anaximander's ideas evoking transformation of species (see chapter B.2).

Although their criticism is based on a similar logic as used by Jacob and Lefèvre, Junker and Hossfeld added new aspects to the list of de Maillet's biological views that are considered as incompatible with modern evolutionary thinking. However, it is doubtful if de Maillet's most characteristics aspects[117] can be used to coin his system as no "true theory of evolution". First, although the transition of aquatic to terrestrial organisms was essential in his system, there are several parts in *Telliamed* describing the evolution of terrestrial creatures, notably the human races (see above). Second, de Maillet obviously defended the idea of an increasing complexity in the transformation of organisms, and although he was inspired by the metamorphosis of an individual (he seems to follow Anaximander in this point), his ideas on species change contain elements that are quite different from a mere transfer of an ontogenetic to a phylogenetic process. Third and more important, although a comparison between modern evolutionary views with those conceived in the past can be useful, the goal of such comparisons should not be a categorization of "true" or "not true" evolutionary hypotheses, as also carried out by Mayr when he coined de Maillet's views as "not genuine" evolutionary (see below). This categorization is misleading both by the implied anachronism of the expression as well as by the arbitrariness of the criteria used.

For instance, Lamarck's biological views can be regarded as lacking a genuine concept of evolution, *if* it is assumed that a genuine evolutionary idea must include a formal concept of natural selection; the same applies to Darwin's biological views, *if* it is assumed that genuine evolutionary views might (a) not overestimate the value of natural selection, (b) not underestimate factors like the complex interplay between structural laws and adaptation, (c) not underestimate the importance of punctuated evolution, and (d) not be formulated without scientific knowledge of genetics.[118] The list can be prolonged to a large extent. Although de Maillet's thesis used an eternal repetition of evolutionary events, the spectrum of evolutionary events which de Maillet described on earth is undoubtedly evolutionary. De Maillet's views on evolutionary events might appear naive according to present knowledge. However, these ideas should be assessed from the perspective of the then state of knowledge.

More relevant than dualistic categorization of early evolutionary ideas is the identification of the influence that these ideas had on other early scholars. We have seen the strong similarity

[117] Although I agree with Junker/ Hossfeld's identification of characteristic aspects of the Mailletian system, I include also the aspect of preformism and cosmogony (plurality of world) implied in de Maillet's evolutionary views, as explained in chapter B.5.

[118] Such premises are often expressed by modern evolutionary biologists. Stephen Jay Gould, for instance, discussed in several influential works (see Gould 2002, passim, and references therein) the gap between orthodox Darwinism and modern evolutionary theory, stressing the non-selectionist forces in evolution.

between the ideas of de Maillet and Goethe on animals adapting to a terrestrial life, and the influence that *Telliamed* had on Kant, Monboddo and Ballenstedt. Also Diderot's atheist and evolutionary ideas were sporadically associated to de Maillet.[119] A further association can be found between de Maillet's interpretation of the development of the feathers expressed in his "flying-fish / bird" passage and Lamarck's following statements on the development of feathers in birds:

> Now we come to a very strange peculiarity which is connected with the environment of these animals. They live more than other vertebrates in the air, and are almost continually rising into it and passing through it in every direction. They have adopted a habit of swelling their lungs with air in order to increase their volume and make themselves lighter; and this habit has caused the organ to adhere to the sides of the chest so that the air within, being rarefied by the heat of the place, has had to pierce through the lung with its investing membranes and to penetrate every part of the body even to the inside of the great bones which are hollow, and to the quills of the large feathers. (Lamarck 2006, 76, translated by Hugh Elliot)

Several of Lamarck's ideas on species changes can be regarded as an improvement of de Maillet's views, especially concerning the changes made in the links between closely related organisms and the lack of mythological creatures in the evolutionary scenarios. Nonetheless, in several cases the influence is still evident, for example when Lamarck envisaged secondary organisms as ancestors of terrestrial species, following strictly the Mailletian schema (see below and Fig. B.2). In the passage above, Lamarck's attempts to explain the evolution of feathers is remarkably similar to de Maillet's scenario on flying-fish / bird. Although he avoided de Maillet's saltatory schema, it is not difficult to recognize in Lamarck's words the strong mechanical process implied in de Maillet's speculations of scales turning into feathers.

[119]There are several hypotheses on the possible contemporary influences on Diderot's concept of species changes. Some authors mention Maupertuis and Buffon (Guyénot 1941, 389-393, 394-401; Roger 1963, 484ff.) in this context. (Guyénot mentioned de Maillet's and Robinet's transformism as "précurseurs fantaisistes" (Guyénot 1941, 389).) Cru states that "the works that attracted Diderot's attention to the question of the origin of animate and inanimate nature were those of his French contemporaries, De Maillet, Bonnet, Robinet, Buffon to some extent, but above all Maupertuis" (Cru 1913, 207). Winter (1972, 46) criticizes Cru's statement, pointing to the fact that the works by Robinet and Bonnet were not formulated before 1761. For her Diderot was also not influenced by de Maillet since the evolutionary concept of both French naturalists diverged essentially. Vartanian (1949) points to the fact that *Telliamed* was published in 1748, short before Diderot published his *Lettre sur les aveugles à l'usage de ceux qui voient* (Letter on the Blind) in 1749; in this letter Diderot formulated for the first time clearly and unequivocally a materialist-atheist position (see Spittler-Massolle 2001). The background on the contemporaries who potentially influenced Diderot's atheist and evolutionary views is discussed by other authors (Crocker 1959 and references therein; Gregory 2007; Winter 1972).

Views on scales that had been transformed into "more developed" structures[120] were also expressed by Johann Christian Rodig, the author of two books with passages on evolution of organisms. Very interesting is Rodig's widely ignored book *Lebende Natur* (Rodig 1801a) published in the same year as his *Naturlehre*[121]. Starting from the idea of the principle of continuity (*scala naturae*) (p. 2-3, 40), he expressed ideas on the evolution of intestines (p. 56), the evolution of snakes (p. 66) and the evolution of mammals from aquatic organisms adapting to a terrestrial environment; he certainly had in mind an analogy between the scales of fishes / reptiles and the scales of mammals of the genus *Manis*: he regarded the single hairs found between the scales of these animals as illustrating the initial process in the evolution of hair (p. 68). As correctly stated by Zimmermann (1953, 254), several of Rodig's evolutionary views may be referred to as "Lamarckism". Amazing are his ideas on the evolution of aquatic mammals: he correctly saw them as originating from terrestrial mammals that returned to the water (p. 96). By recognizing the true nature of secondary aquatic mammals, he was more accurate than de Maillet and Lamarck. The idea of aquatic mammals as former terrestrial creatures became known only 58 years later through Darwin's *Origin of Species.*

To return to de Maillet's and Lamarck's ideas on feathers, Cuvier noted the similarity in their views when he made an allusion to de Maillet's ideas on birds (in the first sentence) when commenting on *Lamarck's* evolutionary ideas:

> Whoever dares seriously suggest that a fish, by staying on dry land, would be able to see its scale crack and change into feathers, and itself become a bird [an allusion to *Telliamed*, RB]; or that a quadruped by penetrating narrow passageways and wiggling along could change itself into a snake, does nothing other than prove the most profound ignorance of anatomy. (Cuvier 1835, vol. 1, 101, translated by R. W. Burckhardt)

Darwin's famous bear-whale statement expressed in *Origin*, which was modified in later editions, was noted immediately after the publication of *Origin* as naive and simplistic as de Maillet's and Lamarck's ideas on the evolution of feathers. Darwin wrote:

> In North America the black bear was seen by Hearne swimming for hours with widely open mouth, thus catching, like a whale, insects in the water. Even in so extreme a case as this, if the supply of insects were constant, and if better adapted competitors did not already exist in the country, I can see no difficulty in a race of bears being rendered, by natural selection, more

[120] On de Maillet's arguments on 'scales' on human skin as demonstrating the aquatic origin of humans see below and footnote 138.
[121] On *Naturlehre* see below; on Rodig being mentioned in connection with de Maillet and Lamarck, see footnote 97. This reference is interesting, as it was known by Charles Darwin.

> and more aquatic in their structure and habits, with larger and larger mouths, till a creature was produced as monstrous as a whale. (Darwin 1859, 184)

This statement appeared also in the first American printings of 1860, but was modified in later editions of his work, as for instance in the second edition, where he wrote:

> In North America the black bear was seen by Hearne swimming for hours with widely open mouth, thus catching, almost like a whale, insects in the water. As we sometimes see individuals of a species following habits widely different from those of their own species and of the other species of the same genus, we might expect, on my theory, that such individuals would occasionally have given rise to new species, having anomalous habits, and with their structure either slightly or considerably modified from that of their proper type. (Darwin 1860b, 184)

This sentence is also found (slightly modified) in the sixth edition (Darwin 1872, 141).

The early associations between Lamarck's and de Maillet's evolutionary views were not necessarily proposed as an attempt to emphasize the role of de Maillet as a pioneer of evolutionary ideas, but more as a strategy to undermine Lamarck's views. The same is true concerning the criticism published after the first publication of *Origin*, on mermaids and other mythological creatures[122] and de Maillet's passages on flying-fish / bird to undermine Darwin's ideas. One example of such a strategy making an association between Darwin's bear / whale passage and de Maillet's flying-fish /bird can be found in a review of the *Origin* published in the *Edinburgh Review* (Owen 1860).[123]

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[122] For an investigation on the role of mermaids and other mythological creatures in late 19th century criticism to Darwinism see Brink-Roby (2008).

[123] Owen wrote:

> If the ursine species had not been restricted to northern latitudes, we might have surmised this to have been one of the facts connected with 'the distribution of the inhabitants of South America,' which seemed to Mr. Darwin, when naturalist on board H. M. S. Beagle, 'to throw some light on the origin of species.' But the close resemblance of the style, and of the tone and frame of mind which could see no difficulty in the adequacy of the above-cited circumstances of 'external conditions, of habit, of volition,' to change a bear into a whale, to those exemplified in the *Philosophie Zoologique*, point strongly to the writings of Lamarck as the true suggestor of Mr. Darwin's views of animated nature. We look, however, in vain for any instance of hypothetical transmutation in Lamarck so gross as the one above cited; we must descend to older illustrators of the favourite idea, to find an equivalent case of the bear in pursuit of water-insects, and we find one in the following: [*text of de Maillet on fish transforming into bird*].

Owen's statement is available online in *The Victorian Web* (http://www.victorianweb.org/science/science_texts/owen_review_of_origin.html#sixteen, accessed on 26 December 2013). On early statements on Darwin's bear / whale statement see the investigation by Soren Lovtrup's controversial book *Darwinism: Refutation of a Myth* (Lovtrup 1987) in which he repeated the unfair criticism formulated by Kohlbrugge (1915) (see above) and criticized the gradualism implied in neo-Darwinian hypotheses.

One influential work in the *Telliamed* discussion is Albert V. Carozzi's excellent commented edition of *Telliamed* [De Maillet, 1968b]. The importance of this work is because the investigations carried out by Neubert (see chapter B.2 and B.3) did not lead to a German (or French) historical-critical edition of *Telliamed*, so that Carozzi's is certainly the most consulted *Telliamed* edition since its publication. Consequently, his opinions on de Maillet's biological views flowed (and still flow) regularly in the discussion on Telliamed, reinforcing the picture released before 1968.[124]

In this work, Carozzi repeated the classical opinion of de Maillet's evolutionary ideas as fantasies:

> This cosmological discussion is followed by a long and fanciful section about the marine origin of plants, animals, and mankind, their transformation into terrestrial equivalents, and the propagation of species by seeds. Although the last discussion contains more fantasy than scientific truth, it is of fundamental importance because it integrates the theory of the diminution of the sea into a broader framework, giving to the entire work the character of a cosmological system. (Carozzi in De Maillet 1968, 3)

In another part of the work he added to a certain passage by de Maillet[125] a footnote: "This statement that extinct species could reappear in the future under favourable circumstances demonstrates that de Maillet advocated only transformation and had no concept of evolution as such" (Carozzi in De Maillet 1968, 402-403).

[124] As often stated in the present chapter, the positive evaluations by Kohlbrugge and Tschulok are based on in-depth studies, but these works are usually not considered in the modern discussion on *Telliamed*.

[125] De Maillet wrote:

> These species which we know have been lost for our globe, like that of the giants who were seventy-five-feet tall and vanished from earth, certainly survive in the sea. Or their seed still occur in the air surrounding it and therefore could reappear again any day (De Maillet 1968, 229).

As we will see, Carozzi regards this passage as an indication that de Maillet did not have a true concept of evolution, an evaluation which I criticise for several reasons. In my opinion, de Maillet's words in the quotation above indicate a much more relevant aspect of his system: that de Maillet was rigorously consistent with his views on evolution expressed in other parts of his work. It is not very productive to get involved in a pure semantic discussion on an essential difference between the words "evolution" and "transformism. I defend the view that de Maillet *had* definitively a concept of species change over time. He was right concerning the crucial aspect of his evolutionary concept (in the sense of negating immutability of species and denying life created by a God). However, almost all details of his system are from today's point of view wrong, since they imply a high degree of preformationism, a concept which was only discarded in late 19th century (Jahn 1998). Instead of denying that de Maillet had a concept of evolution, as it is usually done in the literature, it would be more precise to state that he proposed a preformistic evolution, in which the idea of eternal recurrence and panspermia was presented within a discussion on plurality of worlds.

As specialist in history of geology, Carozzi focused more on the geological part of *Telliamed*, as stated by himself.[126] It is therefore not surprising that Carozzi's s opinion on de Maillet's biological views strongly resembled the views expressed by earlier authors, as John C. Greene in his book *The Death of Adam: Evolution and Its Impact on Western Thought*. In a note Greene wrote succinctly:

> Despite the novelty of his views and his rejection of the Deluge as an explanation of terrestrial phenomena, Demaillet was more classical than modern in his view of nature. Eternal recurrence, not evolution, was his theme. Moreover, by casting his speculations in the form of a romance he lessened their appeal to men of science. Whether Buffon drew on him is doubtful, since Buffon's theory of the earth, though not published until 1749, was composed several years earlier. (Greene 1961, 338)

This statement resumes two common evaluations of de Maillet's biological views. As we will see, his evolutionary ideas are exposed on the one hand as not modern; on the other hand the influence of his biological ideas on other authors is considered as irrelevant,[127] in view of the dialogue form of his system or in view of what are considered the fantastic aspects of his work.

The definition of criteria to evaluate early ideas is often associated with conceptual problems that are hard to solve without using tautological arguments. In fact, historical events are often very complex in nature, making it difficult to argue objectively about how "scientific" an idea might be using modern perspectives. An example of this difficulty is criticism by Carozzi, Greene (and Mayr, see below) directed against de Maillet's ideas of organisms migrating in space (eternal recurrence), which de Maillet thought was possible because the organisms passed from one planet to another in the form of "seeds" in the universe. How useful it can be to evaluate de Maillet's concept of germ-development having in mind modern notions of plant and animal gametes? To understand de Maillet on this topic, we have to understand

[126] Carozzi was confronted with an enormous work in his efforts to integrate for the first time the multiple facets of de Maillet's contribution into a theory of the earth. For this purpose, he commented on Telliamed "with particular reference to its geological significance" (Carozzi in De Maillet 1968, 5).

[127] Interestingly, Greene's criticism concerning eternal recurrence is diametrically opposed to the criticisms formulated by other authors who stress the aquatic / terrestrial transitions as a high degree of saltation for some of these events. The fact that both critiques are regularly represented in the literature without reference to this contradiction is insightful, since it shows how little these judgments are based on a careful analysis of the *whole* Mailletian system. Furthermore, some authors defend a modified form of Greene's views by denying evolutionary views in *Telliamed* but recognizing de Maillet as a precursor of later evolutionists. This position is for instance defended by Garcia Cruz when he concludes that "although de Maillet does not speak in evolutionary terms (*términos evolutivos*), we can consider him a precursor of biological transformism". He saw de Maillet's influence as "evident, albeit implicitly, in Lamarck" (García Cruz 1997, 9, my translation), a view also defended by Tschulok (see below) and which I likewise consider as probable.

particularly the germ concept expressed in the book *De rerum natura* written by the Roman poet Titus Lucretius Carus (ca. 99-55 BC). Lucretius' book is the most extensive defence of the Epicurean philosophy and the most detailed exposition of ancient atomic cosmology and cosmogeny, which originated with Democritus and Leucippus (Lukrez 1981). From this work de Maillet borrowed the ancient atomistic concept of a dynamic universe with several worlds.[128] For Lucretius[129] and de Maillet, the term "germ" included organismic and non-organismic elements and was intrinsically related to the idea of atoms – again a term which cannot be viewed from a perspective of modern concepts. The strong similarity with the ancient Greek atomism allows interpreting *Telliamed* as a work conceived in the materialistic tradition of the Epicurean philosophy. De Maillet merged the atomism with Descartes' ideas on the evolution of cosmos, using geological arguments to corroborate his ultraneptunian[130] theory of the development of the Earth. Although De Maillet's ideas on organismic evolution are unique in this time by the extent of his arguments, he could borrow the notions of organismic plasticity already expressed by Epicurus and Lucretius (Bender 1999b, 9-12).

Carozzi's statement of de Maillet as defending "transformation instead of evolution" is common place in the literature. And although the term is rarely defined clearly,[131] it is often used to separate some evolutionists - often Darwin (or Darwin and Lamarck) – from precursors of this idea.

It is well known that prior to the widespread dissemination of the evolutionary idea after the publication of *Origin*, the term "evolution" was often used in connection with embryological development (Bowler 1989, passim). Darwin did not use the word „evolution" in the first edition of *Origin* until the last line which reads:

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[128] For an overview of Lucretius' role in the plurality of worlds-discussion see Bender (1999b, 8-14) and references in next footnote. See also Zeller on "Greek precursors of Darwin" (the translated title) (Zeller 1879).

[129] (Lukrez 1981, book II, 951-1022, book V, 722-824); see also Bender (1999b, 9-12). Zimmermann (1953, 315) indicates that *Telliamed* adopted the view of the ubiquity of very small seeds already advocated by the Stoics.

[130] De Maillet mentioned several times an Arabic author named Omar-al-Khayyam who was apparently also treating at great length the idea of the diminution of the sea around A.D. 1100. Carozzi wrote on a possible influence on de Maillet's views: "On the basis of the Maillet's own candid description, Omar-al-Khayyam's theory of the diminution of the sea was almost identical to his. Such statement raises the question if de Maillet did not get his original ideas from the books on natural history (now lost) written by this famous Arabic philosopher which he might have read in Cairo or during any of his numerous travels in the Middle East" (Carozzi in De Maillet 1968, 13). For an investigation on the diminution of the sea by 18th century naturalists (including Swedenborg and de Maillet) see Rappaport (1997, 226-234)

[131] To be more precise, the term "transformism" in biology can be used in at least three ways. It is used as (a) a synonymous of "evolution", for instance in dictionaries (Buarque de Hollanda Ferreira & Baptista da Luz 1987); (b) designates evolutionary ideas expressed prior to the time when the term "evolution" began to be used in connection with the concept of species changing over time; and final, (c) to separate certain evolutionists from their precursors; (b) and (c) are explained below.

> There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved. (Darwin 1859, 490)[132]

From the first until the fifth edition of *Origin*, Darwin referred to evolution with different expressions, as "transmutation of species", "course of descent", "descent with modification", "ongoing changes". The word "evolution" in the sense of "transmutation of species" was popularized by Herbert Spencer,[133] and his influence reached also Darwin, who used the terms "evolution" and "evolutionists" in the sixth edition of *Origin* (Darwin 1872, 189, 201, 202, 215, 282).

Although the shift in meaning of the word "evolution" seems to be a reasonable justification for using the term "transformism" to designate evolutionary ideas expressed in pre-Darwinian natural sciences, there is a more subtle reason for the use of this word: as a convenient expression for the categorization of pre-Darwinian evolutionary views as "not modern", or "less scientific". To be sure, I share the opinion of most historians that Darwin's evolutionary ideas represent a landmark in science, and I am convinced that there are several strong arguments which might justify the originality of Darwin's work.[134] However, there are several problems in attempts to draw a clear line between Darwin and naturalists expressing evolutionary ideas before 1859 when these attempts do not consider adequately historical facts. For instance, when strictly employing the term "evolution" to designate the nature of transformist views, Darwin might be considered as not a "true" evolutionist, during the first to fifth editions of *Origin*, but merely as a "transformist", an evaluation which might change only with the sixth edition, where he began to use the terms "evolution" and "evolutionists" (Darwin 1872, 189, 201, 202, 215, 282). The obvious nonsense implied in this statement shows how difficult it is to use a specific terminology to *designate* an idea, which often implies a great degree of oversimplification, instead of considering the *development* of ideas,

[132] In the second edition, the phrase "by the Creator" was added to read: "having been originally breathed by the Creator into a few forms or into one" (Darwin 1860b, 490).

[133] Although Spencer's essay *The Development Hypothesis* first published anonymously in 1852 (Spencer 1891, vol. 1, 1-7) is usually quoted to demonstrate that he used the term "evolution" as equivalent to transmutation of species before 1859, Bowler pointed out that the expression "Theory of Evolution" only appeared in the later versions of the essay - the original 1852 essay refers to the "the theory of Lamarck and his followers" (Bowler 1975b); on Spencer as evolutionist see Bowler (1975b; 1995).

[134] Elsewhere (see Fig. B.2) I will propose that one of the main features of Darwin's evolutionary ideas when compared with his precursors was the fact that Darwin recognized that secondary aquatic organisms did not immediately descend from aquatic ancestors, an insight that has proven to be extremely favourable for his system; the only exception I could find are the views expressed by Johann Christian Rodig in his book *Lebende Natur* (Rodig 1801a, 96).

which is basically a highly complex task demanding more careful statements on what might be considered as "scientific" and what not.

The alleged discrepancy between de Maillet's geological and evolutionary views

There is an important aspect of Carozzi's judgment implied in his designation of de Maillet's evolutionary views as a "long and fanciful section" which "contains more fantasy than scientific truth" (see full quotation above). Carozzi did not justify these statements, and his negative evaluation contrasts drastically with his views on the geological aspects of *Telliamed*.

Similarly, after acknowledging de Maillet's contribution to geology in his book *The Growth of Biological Thought*, Ernst Mayr added following sentence: "Since there is always merely a transformation of a previously existing organism into a new form, a concept of genuine evolution did not exist for de Maillet" (Mayr 1982, 312). More than 100 years before, in an article entitled *Evolution* published in the *Encyclopaedia Britannica*, Thomas Huxley used almost the same words as Mayr to describe de Maillet's views of species changing over time, reaching, however, a completely divergent conclusion about the Mailletian system: "For De Maillet not only has a definite conception of the plasticity of living things, and *of the production of existing species by the modification of their predecessors"* (Huxley 1878, 748, italics added) (see full quotation below).

The discrepancy between Carozzi / Mayr's and Huxley's evaluations can be explained by the fact that the former stressed the aspects of de Maillet's system which are *wrong* from a modern point of view, while Huxley judged the same system having in mind the *revolutionary insights* de Maillet introduced in the natural sciences of his time.

I regard the often expressed dualism "de Maillet's geology and cosmogony = rational / de Maillet's biological views = irrational" as highly questionable, to put it mildly. From an objective point of view, the geological / cosmogony chapters are not more or less scientific (or more or less fantastic) than the biological views of the last parts of the work. As a historian of geology, Carozzi was aware that planets do *not* evolve within a Cartesian system of vortices (as proposed by de Maillet), that celestial bodies are *not* involved in an endless process of alternations between luminous and dark phases, that the globe was *not* entirely covered by sea water and therefore there was *no* gradual and global diminution of the sea, that consequently all of de Maillet's arguments elaborated specifically on this process were equally *wrong*. Furthermore, Carozzi knew that de Maillet's estimation of the long duration of

geological time was strongly inspired by de Maillet's *wrong* specific views of celestial bodies been constantly recycled in an eternal universe.

Why are de Maillet's geological views not regarded– to use the same expressions as in connection to de Maillet's evolutionary views – as fanciful or the product of the imagination of a folly author? The reason lies in several new aspects that de Maillet brought into natural science, such as his emphasis on gradualism, his insistence in considering a long geological time scale, his use of inductive methods, his emphasis on the planet itself and its inhabitants when discussing geological issues, to mention a few. The fact that de Maillet's evolutionary views are often regarded as inferior to his geological system is not based on an objective evaluation of the facts, but is influenced by an anthropocentric perception of his ideas. This subject cannot be discussed in detail here, so we will confine the analysis to a single example related to arguments expressed by de Maillet and Buffon, concerning what both erroneously believed to be a theoretical possibility that mammals might be able to return to an aquatic life and "breathe" in a way analogous to a foetus in the uterus.

It is important to note the possibility that Buffon knew *Telliamed* and was strongly influenced by this work. This influence was assumed, for example, by the contemporary Lamoignon de Malesherbes (1721-1795). He pointed out that *Telliamed* was such a famous manuscript in this time that no educated man could have ignored its existence and no one working on the theory of the Earth could not have consulted it (Malesherbes 1798, vol. 1, 242-243); [135] see also the passage in which he refers to the fact that *Telliamed* circulated as a manuscript for 20 years among all educated people of this time (Malesherbes 1798, vol. 1, 222). Malesherbes specifically pointed out to similarities of Buffon's geological ideas to the views expressed in *Telliamed*: "What therefore belongs to M. de Buffon in this theory of the earth?" (Malesherbes 1798, vol. 1, 240). [136]

Buffon started from the idea that the foramen ovale in the foetal heart is not closed immediately after birth and consequently a part of the blood may continue to pass through that aperture. (He was not wrong in this point. The foramen ovale closes usually within a few days or weeks after birth. In several cases, however, this process did not occur.[137]) He thought that

[135] Telliamed [...] c'étoit un manuscrit si fameux qu'il n'étoit pas permis à un homme de lettres d'en ignorer l'existence, ni à un homme qui travaille à la théorie de la terre de ne l'avoir pas consulté.
[136] Qu'est-ce donc qui appartient à M. de Buffon dans cette théorie de la terre?
[137] It is estimated that 20-35-% of individuals live with a patent foramen ovale (PFO) (Wilmshurst & de Belder 1994), a remnant of the foetal foramen ovale in the atrial septum through which some blood flows between the left and the right atria. The PFO is clinically associated with different problems, among others with

(due to this possible persisting opening of the foramen ovale) a new-born child might sustain a privation of air for a considerable time without losing its existence. Based on this working hypothesis, he carried out experiments in 1739 with new-born puppies, which he described as follows (quoted from a translated edition of his *Histoire naturelle*):

> I put a pregnant bitch, of the large greyhound species, just as she was about to litter, into a tub filled with warm water, where after fastening her in such a manner that the lower parts were covered with some water, she brought forth three puppies, which were accordingly received into a liquid as warm as they had left. After washing them in this water, I removed the puppies, without giving them time to breathe, into a smaller tub filled with warm milk; I chose milk in order that they might receive nourishment if they required it. In this milk they were kept immersed above half an hour; and when taken out they were all found alive. They began to breathe, and to discharge some moisture by the mouth. Having allowed them to respire for half an hour, I again put them into warm milk, and left them a second half-hour; at the expiration of which two of them were taken out vigorous and seemingly no wise incommoded, but the third appeared rather in a languishing state; this I caused to be carried to the mother, which by this time had produced, in the natural way, six other puppies; and though it had been brought forth in water and had lived in milk one half hour before, and another after it had breathed, it yet received so little injury from the experiment, that it presently recovered and was as strong and lively as the rest of the litter. After allowing the other two about an hour to breathe, I put them once more into the warm milk, in which they remained another half hour. (Buffon 1797, 336-337)

After this experiment Buffon was convinced that "it might be possible, with proper precautions, to keep the foramen ovale from being closed, and thus produce excellent divers, which might live equally in air or in water" (Buffon 1797, 338).

De Maillet expressed similar ideas in *Telliamed*. In the sixth conversation of the printed book, he described the possibility "that one may pass form the respiration of water to that of air and vice versa", as the marginal note to this passage reads (De Maillet 1968, 217). He was convinced that the passage from the respiration of water to that of air is natural, since it is demonstrated by several facts, and believed that the inverse change from the respiration of air to water, although much less frequent, is equally supported by evidence:

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paradoxical thromboembolism occurring during scuba diving (Sykes & Clark 2013; Wilmshurst et al. 1994a; Wilmshurst et al. 1994b; Wilmshurst & de Belder 1994)

> I [de Maillet's mouthpiece "Telliamed"] have read in relation from your country that a Dutch captain called Baker, commanding about seventy years ago a merchant ship named the Swallow and sailing along the coasts of Holland, saw a sea man jump out of the sea onto the ship, in the middle of a group of sailors to whom the captain was talking. Their astonishment was still increased when they heard him speak Dutch, and in that language ask for a pipe of tobacco which was readily granted to him. (De Maillet 1968, 217-218)

In de Maillet's views, this sea man did not evolve primarily in water, as most aquatic organisms described in his system, but was a secondary aquatic organism, descending from a human living as a terrestrial creature:

> He was covered with scales[138], his hands were like the fins of a fish, and he looked about thirty years old. They asked him who he was. He replied that he was a Dutchman, and that, having embarked when eight years old on a ship which had been lost with all its crew, he hand since lived in the sea without knowing how such a thing could have taken place. But perceiving that the captain made a sign to the sailors to get hold of him, he threw away the pipe, and by a spring similar to the first one which had brought him aboard, he jumped back in the sea and was never seen again. (De Maillet 1968, 218)

De Maillet explained that this story, although strange, will seem incredible only to those not familiar with the anatomy of the human body, and who have not taken into account the anatomical and physiological changes taking place when humans are still inside of the womb, where they live "without respiration" (see below) (De Maillet 1968, 218). He continued with a remarkable description of this process:

> The latter [the respiration], which only serves to renew the blood and to carry it through the arteries to all the parts of the body for the preservation of life, is provided by two apertures, which correspond to the four large vessels through which the blood, upon leaving the heart, passes from one vessel to another without entering the lungs. Of those two openings, one is of

[138] Close to this passage, de Maillet made another reference to scales, which he used as part of his arguments towards the origin of man from aquatic creatures:

> There is even in all men an indelible mark that they originate from the sea. Indeed if you examine their skin with one of these microscopes, recently invented, which magnify a grain of sand to the size of an ostrich's egg, you will find it all covered with small scales like that of a carp. Besides, we have several examples of men covered with scales, visible without a microscope, which furthermore confirms such an origin. If, therefore, the men who now inhabit the earth descended from other men who lived originally in the sea, is it not probable, as is demonstrated by the previous observations, that some of them, particularly during their youth, might recover the habit of living in the sea as their ancestors did? (De Maillet 1968, 219-220)

When de Maillet mentioned "men covered with scales, visible without a microscope" he is possibly referring to a medical condition: people with the skin disorder called "ichthyosis" (Greek *ichthyis* = fish) have a skin which somehow resembles the scaled skin of a fish.

> oval shape and called hole of Botal [= foramen Botalli = foramen ovale], from the name of the surgeon who first discovered it a few years ago. The other is called the arterial duct, because of its arterial structure. It arises from the vena cava, passes into the right ventricle of the heart, above the right auricle, and terminates in the pulmonary vein. Its construction is such, that by means of valves, it allows the blood to circulate from the vena cava into the pulmonary vein, but no inversely; therefore, in the foetus, the blood neither passes through the lungs nor enters into the left ventricle of the heart. (De Maillet 1968, 218)

He explained that these two canals dried up and obstructed both when the infant is born and begin to breathe, opening "another and easier path to the blood, in which it circulates thereafter for the whole life" (De Maillet 1968, 219). Since in adults no traces generally remain of these two apertures, which provide for the respiration of the foetus, adults usually are not able to breathe under water. He believed that sometimes these apertures are not completely closed up. That would explain the performance of some famous divers and criminals who did not suffocate by hanging (De Maillet 1968, 219). He rejected the opinion that the latter did not suffocate due to the hardness of the larynx of these individuals, preferring the hypothesis of these men breathing in an analogous manner as unborn humans when living in the womb:

> It is by means of this structural arrangement that sea men and sea calves live in the sea without respiration. There is no doubt, therefore, that the young Dutchman, who lived in the sea without being suffocated, had these two holes still open when shipwrecked at the age of eight, and that he had resumed the habit of living without respiration, as he did in his mothers' womb. (De Maillet 1968, 219)

In his attempts to prove the origin of humans from water, de Maillet expressed what I believe to be the first[139] evolutionary medicine-argument:

> This opinion has not only been adopted by the most famous philosophers of the past centuries, but also leads to several very conclusive statements which demonstrate that men owe their origin to the sea. How many diseases do your physicians cure only by the use of water, either ice cold or warm? Has it not been recognized that it is the most rapid and efficient remedy to extinguish, in a patient's veins, the heat of a fever which consumes him? Has it not been found that, of two runners, if the loser bathes himself and runs again, he will beat his opponent? This is also demonstrated among the Jews by the pool in which lepers were thrown to be cured [.] (De Maillet 1968, 220)

[139] Erasmus Darwin is usually mentioned in discussions on early precursors of evolutionary medicine (see Antolin 2011, and references therein).

As we see, Buffon and de Maillet shared similar ideas concerning the possibility of mammals adapting to an amphibious life through anatomical changes of the cardiovascular system. In the school of morphology established by the French Academy of Sciences in 1666, investigations of comparative anatomy were carried out in connection with the aquatic mammal's ability to stay long periods under water, as explained by Cole:

> They are aware that the seal is not a fish, and is incapable of aquatic respiration, and they are led to assume that it must have an intranarial epiglottis to enable it to feed under water. They also understand that in the mammalian foetus blood is diverted from the right side of the heart to the left through the foramen ovale in order to avoid the lungs [this was known to Galen, and is discussed by Servetus and Harvey], and they draw from this the fatal conclusion that the foetus does not respire. They profess to have found, and, indeed may actually have found, a persisting foramen ovale in the heart of the seal, and they believe that when the animals dives, and remains some time below water, the circulation follows the same course as in the intra-uterine embryo. The fact that the seal is below water only for a relatively short time, whilst the circulation of the foetus remains the same throughout foetal life, should have warned them of the risk of assuming an interruption in the normal circulation every time the breathing organs are cut off from the atmosphere.(Cole 1944, 420-421)

The only difference between de Maillet and Buffon is related to the species they considered as being able to develop cardiovascular structures, enabling them to stay longer underwater: dogs in Buffon, different mammals – including humans – in de Maillet.

The existence of aquatic counterparts in humans is, from a modern point of view, of course completely inconceivable. However, similar ideas were sporadically expressed by scholars in the 17th and 18th century, not long before de Maillet formulated his ideas. For example, in 1654 the Dutch anatomist Thomas Bartholin published the illustration of a skeletal forelimb and a rib from a creature found on the coast of Brazil. He interpreted this organism – probably a manatee (Senter & Snow 2013) – as a specimen of *Homo marinus.* The Dutch naturalist François Valentijn (1666-1727) published in his book *Oud en Nieuw Oost-Indiën* (Valentyn 1724-1726)[140] a large collection of observations to support his belief in the reality of

[140] For an analysis of Valentijn's *Oud en Nieuw Oost-Indiën see* LaBarge (2011) and references therein. Athanasius Kircher believed on the existence of mermaids. In his book on Noah's ark (Kircher 1642) he wrote that anyone who doubts the existence of the creatures needs only to see the skeleton from his museum (see Allen 1949, 186).

mermaids; this work was influential in later speculations on mermaids. Similarly, Monboddo described the amphibious nature of a girl[141] in his *Antient Metaphysics* (Monboddo 1782, 79).

When early and modern authors interpret de Maillet's beliefs on *hommes marins* as a sign of great ingenuity, they often do not take into consideration that de Maillet proposed his evolutionary views at the beginning of the 18th century. It seems that biologists and historians tend to compare de Maillet's ideas with works published middle 18th century, perhaps because *Telliamed* was first published in 1748, after his death, while his system was conceived around 1715. De Maillet grew up in a time in which the classical works were still influential. The light of the cultural movement emphasizing reason and scientific method did not shine with the same intensity on the different areas of the natural sciences. De Maillet developed his system without help from other works where he could have borrowed the specific terminology needed to describe evolutionary processes. Solid concepts on systematics were also absent in this period, and among the few evolutionary ideas available at this time were crude concepts of species changes expressed by authors of the classical period or by theologians in their attempts to explain the dilemma of so many organisms having a place in a rather small Noah's Ark.[142]

Although de Maillet based some of his thoughts on zoological and anatomical publications of the late 17th century,[143] he also used the works of medieval European naturalists which were still influential in his time. In contrast, Charles Darwin and Alfred R. Wallace carried out

[141] Monboddo described the "last step of this progression [from a quadruped and Ourang Outang to men] I likewise saw, and it was a great one" (Monboddo 1795, 33). He referred to Marie-Angélique, the wild girl, "or *fille sauvage*, as the French called her". He interviewed her on 28 March 1765, which was reproduced in an appendix of *Antient Metaphysics*. This is the beginning of the interview:

> This day saw and conversed with Mademoiselle le Blanc (so they called her). — Says that she remembers the country she came from is a very cold country, covered with snow a great part of the year, and the nights very long. That the children there are accustomed to the water from the moment of their birth — that they learn to swim as soon as they can walk; and also to climb trees — and that a child of a year old there will climb up a tree. That they live in little huts above the water like Beavers; and that they subsist very much by fishing. That she was so much in the use of the water, that, when she came to France, she could not live without it; and, at first, was in use to plunge into it over head and ears, and to dwell in it like an Otter, or any other amphibious animal; and afterwards, when she was restrained from that, she always washed her head and hands. That, though she supposes she was a child only about seven or eight years of age when she was carried away, yet, by that time, she had learned to swim, to fish, to shoot with the bow and arrow, to climb and to leap from one tree to another like a squirrel. (Monboddo 1795, 403)

It seems that Monboddo exaggerated the physical strength and aquatic abilities of a rather normal girl who enjoyed swimming and diving.

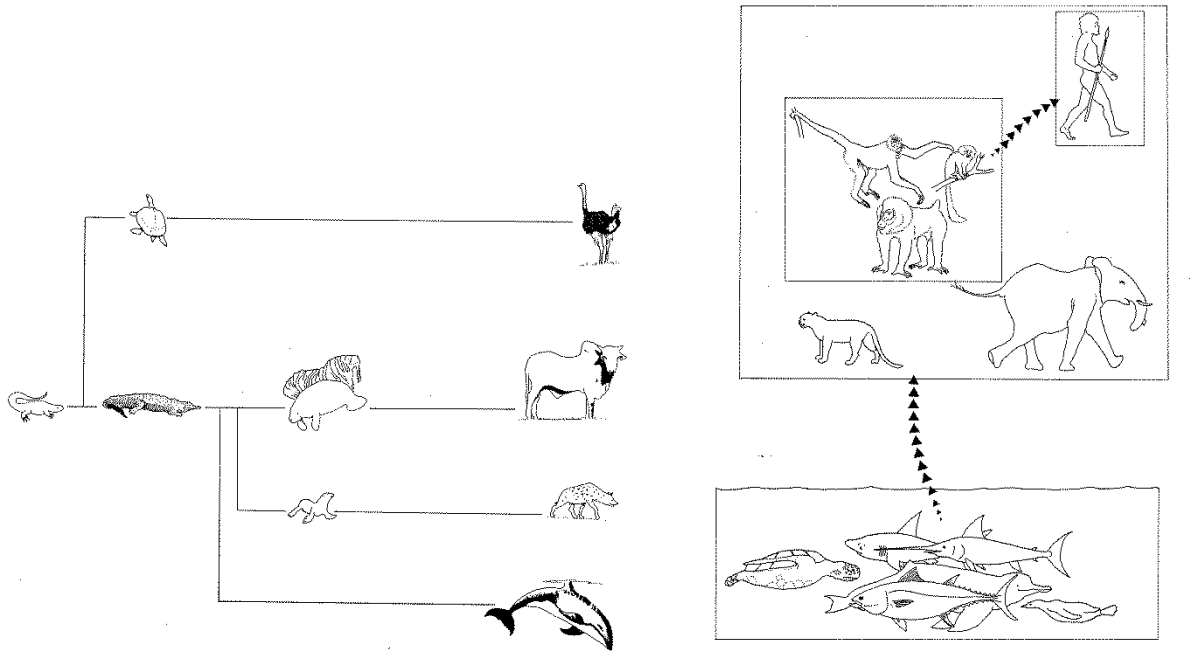
[142] As for instance, Athanasius Kircher (1642) in his book *Arca Noë* (Allen 1949, 182-191; Bourdier 1960; Krause 1880, 219). For a discussion on problems of all animals having place in the Ark from the point of view of young earth creationists see Whitcomb and Morris (1978, 63-88).

[143] See above on de Maillet's ideas on anatomical and physiological aspects related to an amphibious life.

research at a time when biology was evolving to an unprecedented extent. Works published in the 19th century by naturalists like Alexander von Humboldt, Linné, Richard Owen, Karl von Baer, Cuvier and Thomas Huxley led to an unequivocal attenuation away from the influence of ancient naturalists. The terminology needed to describe the design of various species of animals were not only supplied by naturalists, but also by proponents of natural theology like William Paley's book *Natural Theology* (Paley 1802), a work which strongly influenced Darwin (Darwin 1958, 59). Thomas Robert Malthus' *An Essay on the Principle of Population*, first published in 1798, had an immense influence on Darwin's and Wallace's views on the role of natural selection (Darwin 1887, vol. 1, 83; Wallace 1905, vol. 1, 361-363).[144]

Although *Telliamed* reflects the influence of ideas expressed prior to the Enlightenment, it is from an objective point of view unjustifiable to stress this aspect of his work negatively when considering what de Maillet actually achieved: the first extensive system of species change ever proposed by a naturalist. There is another interpretation of de Maillet's use of mythological creatures. As de Maillet regarded all terrestrial organisms as having counterparts in water, it would be inconsequential to exclude humans from this system. By taking the risk to include *hommes marins* in *Telliamed*, he avoided the strong anthropocentrism bias - humans as the only organisms *not* evolving from aquatic counterparts. By doing so, however, he was perceived by most naturalists more as a highly speculative layman than as a serious naturalist. As a result, scholars who recognized both the value of the Mailletian system, as well as its problematic aspects, were inclined to adopt large parts of his views and reinterpret the system without referring to him. An example is supplied by Lamarck, who deviated from the Mailletian system by envisaging primeval man evolving from an ape coming out of the forests and entering into an open environment (see below and Appendix D). However, in his views on the evolutionary path of several other living organisms, Lamarck is much closer to the ideas propagated by de Maillet than to Darwin's evolutionary hypotheses when he defended a version of de Maillet's thesis of counterparts (see Fig. B.2).

[144] This work was basically conceived as to demonstrate the effect of natural selection in human populations. It is well known that Darwin and Wallace recognized the far-reaching meaning of Malthus' arguments (Richards 2008; Schweber 1977). Both naturalists adopted independently from each other Malthus' concept of human populations being regularly checked (selected), merged it with the concept of evolutionary changes occurring over long periods of time and applied the resultant system to all organisms.



(A) (B)

Figure B.2 Lamarck's generals views on aquatic organisms changing to a terrestrial environment – here depicted schematically in (A) – are an adaption of de Maillet's views on aquatic beings as counterparts to terrestrial organisms. The most important difference to de Maillet's concepts concerns Lamarck's decision to depict humans as descending from an ape (B). Darwin was the first known[145] evolutionist who fully recognized that, for example, whales and crocodiles are secondary aquatic organisms. In his views on the evolutionary path of several other (non-human) living organisms, Lamarck is much closer to the ideas propagated by de Maillet than to Darwin's evolutionary hypotheses.

As it is often the case in historical investigations, we cannot decide here if Lamarck knew de Maillet or not, as he did not mention *Telliamed* in connection with his own ideas. It is of course difficult to assess which works were consulted by early naturalists – the case of Goethe, who demonstrably borrowed *Telliamed* (as shown above, chapter B.3) is exceptional. Taking into consideration the popularity of de Maillet's ideas in France in his time, it would be certainly much more difficult to defend the thesis that Lamarck did *not* know de Maillet's ideas, rather than the contrary. Sinai Tschulok, a specialist[146] on Lamarck, states that some passages of Lamarck (he did not specify which ones) are almost word for word compilations of de Maillet's work (Tschulok 1938, 336). A structural and thematic comparison of the two works is required. However, as Tschulok already noted, although Lamarck knew Buffon,

[145] See chapter B.4.3 on Johann Christian Rodig's views on aquatic mammals as descending from terrestrial ancestors.

[146] This authors is rather unknown by modern Lamarck's scholars; however, he is highly praised for his investigations on Lamarck's work by historians working in German speaking countries.

Bonnet and de Maillet, all these authors developed quite different evolutionary ideas. The most crucial differences between Lamarck and other French authors, so Tschulok, lie both in the corroboration of his system through physiological processes, which he describes through chemistry, and that Lamarck did not find it necessary to prove the reality of these processes, a fact that Tschulok believed was "the most characteristic aspect of Lamarck's system when compared to other authors" (Tschulok 1937, 88, my translation). Despite these differences, several early authors pointed to the similarities between de Maillet's and Lamarck's evolutionary ideas, or mentioned both authors in the same context; only a selection of examples can be given here.

When commenting on de Maillet's views on organismic evolution, Cuvier wrote: "He is the one who first envisaged the possibility of a transformation of marine species into terrestrial species"[147] (Cuvier 1841, 79). He pointed out that this theory "has been reproduced in many ways by modern authors"[148] (Cuvier 1841, 79), and that there are "on this subject four or five systems, which are nothing other than amendments of de Maillet's system" (Cuvier 1841, 79).[149] He mentioned Jean-Baptiste-René Robinet's *Considerations philosophiques de la gradation naturelle des formes de l'etre* (Robinet 1768) (according to Cuvier "Le plus singulier de ces systèmes"[150] (Cuvier 1841, 82)), Johann Christian Rodig's *Naturlehre* (Rodig 1801b)[151] and Lamarck's *Hydrogéologie*, *Recherches sur les corps organisés* and *Philosophie zoologique* (Cuvier 1841, 85ff). Similarly, Bertrand associated de Maillet's ideas on human evolution with Lamarck's ideas: "Although Maillet's opinion on the origin of the human race

[147] C'est lui, qui le premier, a avancé la possibilité de la transformation des espèces marines en espèces terrestres.
[148] Cette théorie a été reproduite de beaucoup de façons par les auteurs modernes [.]
[149] Il y a sur cette matière quatre ou cinq systèmes qui ne sont guères que des modifications de celui de De Maillet.
[150] Cuvier judged correctly - Robinet's ideas are quite singular. Basically, he interpreted the *scala naturae* in terms of a natural philosophical transformism characterised by a high anthropocentrism and a radical continuity principle. In his system the organisms are not transformed from one species to another. Rather he believed that the more progressive forms only could be created after the less progressive forms emerged. In this concept, all organisms are failed attempts to be transformed in the most perfect creature – humans. His natural philosophical world view allowed him to believe that "living stones" can be transformed into fossils; this account for the fact, so Robinet, that we can find stones in the form of heart, kidney and skull, things that he interpreted as natural attempts towards the formation of humans (Robinet 1768, passim). See Rappaport (1997, 105-135) and references therein for views on fossils in late 17th and first half of 18th century.
[151] The interesting parts of his *Naturlehre* (Rodig 1801b) are the two last chapters entitled *Analogien* (pp. 172-176) and *Allgemeine Naturgeschichte der Erde* (general natural history of the earth) (pp. 1762-186), especially on p. 185, where he specifically mentioned organismic evolution taking place on a large time scale. As implied in the title of the last chapter, Rodig makes frequent references to ideas expressed by Immanuel Kant. It is interesting to see that Rodig's views on transformism are – similar to de Maillet and Chambers – inspired by the discussion on the evolution of the universe; on Rodig's evolutionary views expressed in another of his books see above; on an author mentioning Rodig, Lamarck and de Maillet in the same context already in 1838 see above.

is similar to the one of a contemporary famous naturalist [footnote: M. de Lamarck], I hardly dare to mention any such opinion, since I have a feeling it was ridiculous and shocking" (Bertrand 1833, 14, my translation).[152] Charles Lyell mentioned *Telliamed* as a precursor of evolutionary ideas in his *Principles of Geology*, although he mistakenly mentioned Jean-Claude Delamétherie (1743-1817) as the authors of this work:

> These speculative views [on the progressive evolution of organisms defended by Lamarck] had already been, in a great degree, anticipated by Delamétherie [sic] in his Teliamed [sic], and by several modern writers, so that the tables were completely turned on the philosophers of antiquity, with whom it was a received maxim, that created things were always most perfect when they came first from the hands of their Maker, and that there was a tendency to progressive deterioration in sublunary things when left to themselves. (Lyell 1832, vol. 2, 11)

These mistakes were corrected in further editions of the work (see, e.g., 5th ed., vol. 2, 373) and in his book *The Antiquity of Man* (Lyell 1863, 573), where he wrote:

> [H]e [Lamarck] also shows that he was deeply impressed with a belief prevalent amongst the older naturalists, that the primeval ocean invested the whole planet long after it became the habitation of living beings; and thus he was inclined to assert the priority of the types of marine animals to those of the terrestrial, so as to fancy, for example, that the testacea of the ocean existed first, until some of them, by gradual evolution, were improved into those inhabiting the land. These speculative views had already been, in a great degree, anticipated by Demaillet in his Telliamed, and by several modern writers [.](Lyell 1863, 573)

I did not investigate possible sources of Lyell's positive views on *Telliamed*. It is known that some early authors evaluated de Maillet more or less positively in geological treatises, as did Alexandre Bertrand in the introduction of his *Lettres sur les révolutions du globe* (Bertrand 1833, 10-15).[153] In his book, *The Origin of Species or, The Causes of the Phenomena of Organic Nature*, Thomas Huxley referred briefly to *Telliamed* as follows: "So far, the facts of palaeontology are consistent with almost any form of the doctrine of progressive modification; they would not be absolutely inconsistent with the wild speculations of De Maillet, or with the less objectionable hypothesis of Lamarck" (Huxley 1863). In a later work, he expressed himself quite positively on de Maillet's evolutionary views; as I gave above only a fragment of his statement, here is the full quotation:

[152] Quoique l'opinion de Maillet sur l'origine de la race humaine ressemble à celle d'un célèbre naturaliste de nos jours, je n'ose presque la faire connaître, tant je sens qu'elle paraîtra ridicule et choquante ».
[153] See full quotation above, where Bertrand associated de Maillet's hypotheses with Lamarck's views.

> Considering that this book was written before the time of Haller, or Bonnet, or Linnæus, or Hutton, it surely deserves more respectful consideration than it usually receives. For De Maillet not only has a definite conception of the plasticity of living things, and of the production of existing species by the modification of their predecessors; but he clearly apprehends the cardinal maxim of modern geological science, that the explanation of the structure of the globe is to be sought in the deductive application to geological phenomena of the principles established inductively by the study of the present course of nature. (Huxley 1878, 748)

Similarly, Armand de Quatrefages de Bréau also was very positive on de Maillet:

> I just mentioned a name that has the unpleasant privilege to almost always and everywhere elicit a mocking smile. When I count him to the precursors of the ideas that I will discuss, I'll do it not with the intention to discredit his ideas. I do it mainly because this name appears regularly in controversies on the topic discussed here, and I also do it because it always seemed to me that this author was treated unfairly. Without wishing to rehabilitate him beyond his merits, I think that it would be useful to show why he was so violently attacked, not only by its natural enemies, but also from those who should actually judge him favourably. (Quatrefages 1870, 19-20, my translation)[154]

A reviewer of *The Brisbane Courier* defended Darwin's claims on originality by attacking Quatrefages' positive evaluation of the Mailletian system:

> In *Charles Darwin et ses précurseurs Français* we see perhaps a tendency to make too much of what had been effected by previous workers in the same field in France. No one can indeed be more candid or even generous than Mr. Darwin in acknowledging the steps by which he had himself been guided in his path of discovery. Still it will never do for England to part with the priority and originality which invest the ideas of natural selection, the struggle for life, and especially the great recent doctrine of pangenesis. We should ourselves incline to class even above these special gains to science what has been done to bring to an issue that which is of so much importance to philosophy in general – the definition of species itself. Upon this latter point we find naturalists of eminence in our own day almost as hopelessly groping for light as their predecessors of the scholastic period. First on M. de Quatrefages' list of predecessors of

[154] Je viens d'écrire un nom qui a le privilége [sic] désagréable de provoquer à peu près toujours et partout un sourire dédaigneux ou railleur. Cependant si je l'inscris parmi ceux des précurseurs des idées que je vais discuter, ce n'est point avec l'intention de jeter d'avance sur elles le moindre discrédit. C'est surtout parce que ce nom revient ã chaque instant dans les controverses soulevées par l'ordre de conception qui nous occupe ; c'est aussi parce qu'il m'a toujours paru qu'on a été injuste envers cet auteur. Sans vouloir le réhabiliter au delã de ses mérites, je crois utile de montrer pourquoi il a été si vivement attaqué, non-seulement par ceux dont il était en quelque sorte l'adversaire naturel, mais encore par ceux qui semblaient devoir l'accueillir en allié.

> Darwin is De Maillet. Telliamed, the name of the author written backwards, a work of immense ingenuity, but fanciful to a degree which caused it to pass for little more than pleasantry, and which brought upon it the crushing raillery of Voltaire, started the idea of transmutation of species by a kind of adaptation to the surrounding medium, in which was anticipated the landing principle of the system of Lamarck. (Anonymous 1870, 4)

Interesting in this criticism is the association between de Maillet and Lamarck as an obvious attempt to undermine Lamarck's views.

Similar positive views on the scientific value of *Telliamed* to those expressed by Huxley and Lyell were also sporadically expressed by later historians. The Dutch physician, anthropologist, anatomist and historian Jakob Hermann Friedrich Kohlbrugge (1865-1941) and the Swiss (born in the Ukraine) biologist and historian Sinai Tschulok (1875-1945) were decisive opponents of one-sided evaluations of *Telliamed.* In their works (which are widely ignored by modern historians of science), they argued convincingly that *Telliamed* deserves a place as a forerunner of Lamarckism and Darwinism (Kohlbrugge 1912; Tschulok 1938); at least part of Kohlbrugge's motivation of stressing the positive aspects of *Telliamed* was certainly his antipathy towards Darwin and his attempts to undermine Darwin's (justified) claims on originality (see above, footnote 56). Günthart (1928, 22) based his succinct statement on de Maillet's evolutionary views on Tschulok and therefore evaluated *Telliamed* positively.

Walter Zimmermann summarized de Maillet's views in his book on the history of evolutionary ideas, quoting extensive passages of *Telliamed* translated in German (Zimmermann 1953, 310-316). Rather unusually, he did not judge negatively de Maillet's use of mythological creatures in the corroboration of his evolutionary theory, but stressed unconditionally the positive aspects of de Maillet's evolutionary concepts: "B. de Maillet [...] has set out for the first time a clear theory of evolution under the anagram *Telliamed*" (Zimmermann 1953, 311, my translation). Among modern historians, Claudine Cohen, a *Telliamed* expert, investigated the intellectual context in which this work was produced (1989b; 1993; 2011). She defends the idea that the geological, evolutionary and anthropological ideas expressed in *Telliamed* were a progress in natural science in this time (Cohen 1989a); see also (Stott 2013), who emphasizes the positive aspects of de Maillet's evolutionary ideas.

B.5 Conclusion

A historically founded evaluation of de Maillet's ideas is essential, because it opens new perspectives for analysing the emergence of evolutionary ideas. A scientist cannot always satisfy all the expectations of the scientific community in a particular period of time. Individualities – as for example childish naivety or the inclination of unconventional pattern recognition – often do lead to insightful ideas as well as to disappointing concepts. For example, Alfred R. Wallace's reputation suffered from his interest in spiritualism and from certain aspects of his views on human evolution (Kottler 1974). Perhaps it is Wallace's fondness for unusual ideas that could explain why he was influenced by Chambers (see McKinney 1972, 9, 11). This same Chambers was criticized frequently as the author of a flawed book on evolution by more conventional scientists – like Darwin, who confessed that Chamber's book "simply irritated me by the prodigious ignorance and thoroughly unscientific habit of mind manifested by the writer" (Darwin 1887, vol. 2, 188).[155] Chambers and Wallace were open to the idea of evolution, while most naturalists prior to 1859 rejected this concept.[156]

In the present chapter I showed that several views implied in the negative evaluations of de Maillet's evolutionary ideas are essentially attempts to create a clear but quite artificial delineation between scientific and non-scientific ideas. Instead of comparing *Telliamed* directly with the works on evolution published in the 19th century,[157] from a historical point of view, it is more useful to compare de Maillet's system with the evolutionary ideas expressed in the period in which *Telliamed* was conceived, i.e., circa 1690-1715.[158] From this

[155] However, it is interesting to see that the difference in character between Darwin and Wallace did not prevent both naturalists from recognizing the value of Malthus' ideas for the formulation of their hypotheses on natural selection (see above, chapter B.4.3).

[156] For example, it is well known that Thomas Huxley resisted the evolutionary idea not only after reading Chambers' *Vestiges,* but even after Darwin's first attempts to convince him. Commenting on this topic (he referred specifically to the fact that he did not conceive the idea of natural selection), he wrote the famous words: "My reflection, when I first made myself master of the central idea of the 'Origin', was, "How extremely stupid not to have thought of that!"" (Huxley 1887, vol. 2, 197). Although Huxley played an important role in evolutionism, his picture does not hang in the gallery of *first* proponents of evolutionary ideas, but Chamber's and Wallace's do. Also interesting is the role Cuvier played in the debate on evolutionary thought in early 19th century, as Ernst Mayr aptly stated: "Given this background and experience, one might have expected him to become the first proponent of a thoroughly sound evolutionary theory. In actual fact, Cuvier throughout his life was wholly opposed to the idea of evolution (see above), and his arguments were so convincing to his contemporaries that even after his rather early death evolutionism was unable to assert itself in France for the next half century" (Mayr 1982, 364); see also Limoges (1970a).

[157] It should be remembered that the first *Telliamed*-manuscripts were written 145 years before the publication of Darwin's *Origin of Species* and 95 years before Lamarck's *Philosophie zoologique*

[158] The intellectual context in which *Telliamed* was produced was investigated by (Cohen 1989b; Cohen 1993; Cohen 2011). She repeatedly defended the idea that, despite its archaism, the evolutionary ideas expressed in

perspective, the French naturalist stands alone with his transformism, both concerning the elaboration of his system as well as his efforts to corroborate it by rational arguments. I argue that the implicit classification of *Telliamed* as non-scientific, pseudo-evolutionary prose should be abandoned, as it serves the sole purpose of obliterating crucial aspects of the origins of early 18th century evolutionary ideas.

This discussion should not be perceived as an effort to "rehabilitate" de Maillet as an early evolutionist. Such rehabilitation is only secondary[159], if compared with a much more important aspect of the discussion. I argue that the traditional negative opinion of the scientific character of *Telliamed* prevented an understanding of a fundamental aspect of the historical development of evolutionary thoughts in early 18th century: I submit that concepts of species changes and deep time had a crucial impulse from the plurality of worlds-debate. The term "plurality of worlds" or "cosmic pluralism" (or simply "pluralism") is commonly used to describe ideas of the existence of life on other planets. Early thinkers usually regarded "other planets" as "Earth-like planets", and "life" usually as intelligent, mostly "human-like". The debate on the plurality of worlds, with roots in ancient Greece, has been investigated in several historical works and will not be summarized here.[160]

De Maillet's evolutionary ideas are important, because they reveal that 18th century transformism is on the one hand closely linked to the views evoking species transmutation and pluralism expressed by ancient philosophers (Anaximander and Lucretius among others), while on the other hand it is the consequence of the pluralism directly linked to the

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Telliamed – including de Maillet's views on the evolution of man (Cohen 1989a)– represented a progress in natural science at this time.

[159] Please note that I usually do not refer to de Maillet as a "precursor" – this expression evokes ideas of anachronistic interpretation of historical facts. For some reason there is a tendency to refer to pre-Darwinian proponents of evolutionary ideas through the rather naive dichotomy "precursor of Darwin" / "not precursor of Darwin", which goes hand in hand with evaluations on "genuine or non-genuine" evolutionary ideas. The problems with such discussions are that ideas expressed by different authors in different times are very difficult to compare. This applies even to similar ideas expressed by contemporary authors and sometimes even to ideas expressed by the same author in different contexts. One way to circumvent anachronistic interpretations is to focus on the degree of influence a certain idea had on contemporary thinkers; this approach is followed here.

[160] The doctrine of the plurality of worlds is topic of several investigations (Benz 1978; Carré 1974; Crowe 1986; Dick 1982; Dick 1998; Dijksterhuis 1956; Duhem 1914, chapter 20 in volume 9; Fellmann 1971; Guthke 1983; Heffernan 1978; Knight 1967; Koyré 1980a; Kuhn 1957; McColley 1936; McColley & Miller 1937; Oresme 1977; Paul 1986b; Rossi 1972). The impact of pluralism on religious traditions is also extensively researched (Benz 1969; Benz 1977; Benz 1978; Brooke 1977; Coyne 2000; Dick 2000; Dick 2005; Kragh 2004; Kreiner 2011; Nibley 1975; Paul 1986a; Paul 1992; Westfall 1958; Zabilka 1979); for the consequences of the condemnations of 1277 on pluralism see Al-Biruni (1991) and Strohmaier (1991); the connection between plurality of worlds and the emergence of evolutionary ideas is already suggested in an unpublished manuscript (Bender 1999b).

Copernican revolution[161]. The most common metaphor between the Copernican revolution and evolutionism is linked to a curious, immodest parallelism expressed by Sigmund Freud, who saw the Copernican and Darwinian revolutions along with his own contribution to psychoanalysis as decisive blows against "human megalomania" (*menschliche Grössensucht*) (Freud 1922, 323-324); the irony of Freud's statement is speaks for itself. (Although, the comparison between Darwin and Copernicus harks back to earlier sources.)[162] Sporadically, modern authors[163] refer to the analogous impact of both events in science.

However, the specific connection between the *emergence* of evolutionism and pluralism is usually not acknowledged in the literature, since historians specialised in the Copernican revolution and/or in the doctrine of plurality of worlds usually do not follow the implications of these events in the discussion of evolutionary thinking;[164] one interesting exception is Michael J. Crowe's excellent historical treatise on the extra-terrestrial life debate between 1750 and 1900.[165]

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[161] The Copernican revolution was extensively investigated (Bialas 1994; Dick 1982; Dick 1998; Dijksterhuis 1956; Koyré 1980b; Kuhn 1981; Neuser 1994; Pruett 2012; Scheidler 1994; Wolfschmidt 1994; Wolfschmidt 1995).

[162] It is sporadically mentioned that Freud was perhaps inspired by Emil Du Bois-Reymond concerning the comparison with Copernicus, who published in his book entitled *Reden* a reprint of a speech delivered on 25 January 1883 in the *Berliner Akademie der Wissenschaften* (Du Bois-Reymond 1912). In this talk (a Darwin's obituary), he called Darwin "the Copernicus of the organic world" (*der Kopernicus der organischen Welt*). Ernst Haeckel (1908, 39) indirectly accused Du Bois-Reymond of plagiarism, since Du Bois-Reymond used exactly the same words expressed by Haeckel fifteen years before in one of his own talks.

[163] For an example of a link between Copernican revolution and evolutionism see Theodosius Dobzhansky's famous essay *Nothing in Biology Makes Sense Except in the Light of Evolution,* where the geocentrism of Shaikh Abdul Aziz bin Baz is used in the introduction; the paper is conceived as a criticism to creationism (Dobzhansky 1973). Another example is supplied by Francisco J. Ayala (2007) who refers to Darwin as the author who "completed the Copernican Revolution by drawing out for biology the notion of nature as a lawful system of matter in motion that human reason can explain without recourse to supernatural agencies" (Ayala 2007, 8567). Ayala is referring to the conflict raised between Paley's natural theology and Darwin's evolutionism. He compared the Copernican/Darwinian revolution in order to stress the importance of Darwin's ideas to solve the conflicts raised between natural theology and evolutionism. My own argument – that emergence of evolutionary thought is intrinsically related to ancient and Copernican pluralism – refers obviously to an earlier aspect of the link between evolutionism and Copernican revolution.

[164] There are of course several well-known implications of pluralism on evolutionary views after 1859. Insightful are for instance Carl du Prel's books *Der Kampf ums Dasein am Himmel* (1874), *Die Planetenbewohner und die Nebularhypothese (1880)* and *Entwicklungsgeschichte des Weltalls (1882),* in which he transferred Darwinism to astronomy, or Alfred R. Wallace's *Man's Place in the Universe: A Study of the Results of Scientific Research in Relation to the Unity or Plurality of Worlds* (1903), in which he expressed his anthropocentric worldviews. Implications on evolutionism are also evident in the ideas expressed by Richard A. Proctor, Camille Flammarion, Percival Lowell, and many others scientists in the second half of 19th century (see above for explanations and references). However, as stated, most investigations on the topic "plurality of worlds" do not mention de Maillet, although *Telliamed* is mentioned in Flammarion's influential book *La pluralité des mondes habités*; I consulted the second ed. (Flammarion 1864, 477); he also discussed *Telliamed* extensively in his book *Dieu dans la nature* (Flammarion 1867, 439-442).

[165] It is interesting that Crowe does not follow de Maillet's pluralism; he merely mentions de Maillet as a passing thought that Diderot was partially influenced by de Maillet (Crowe 1986, 135, 579), referring to

The Copernican revolution had a stronger and above all earlier link to evolutionary thoughts than usually assumed. As we saw, de Maillet was obviously influenced by the elements of atomistic doctrine expressed by Lucretius (c. 96-55 BC), and combined these ancient views with the cosmogony defended by Descartes and the pluralism of his friend Fontenelle. De Maillet used elements[166] in his system that are often regarded as proving his ingenuity and demonstrating that his system was a typical construct of early 18th century *Naturphilosophie*.

However, what is usually regarded as non-scientific elements in de Maillet's system can be interpreted from a different perspective. I submit that de Maillet's so-called naive or fantastic views on real or imaginary aquatic organisms as counterparts to terrestrial creatures provided him with an unusual dichotomic pattern in the organismic world. His emphasis on this doubtful dichotomy had two main consequences: on the one hand he was able to envisage an erroneous, but insightful phylogenetic link between (all) aquatic organisms as ancestors of terrestrial counterparts; on the other hand he was able to transfer the concept of stellar evolution (again wrong, but insightful) to the realm of living organisms. By using epistemological discrepancies as bridges between distantly related taxa, he formulated what can be regarded as the first lengthy evolutionary concept. De Maillet's envisage of the evolutionary process in vast spatial dimensions and in events of eternal recurrence certainly forced him to assume an extended time scale, which he integrated with his geological ideas.[167] Although his ideas are quite different from modern evolutionary views, I showed that his system influenced several naturalists in the 18th and 19th century that are often regarded as important precursors of the evolutionary thought.

Vartanian's (1949) investigation on Diderot (on Vartanian's views see above, chapter B.4.3). Crowe and other experts on pluralism cannot be blamed for not stressing de Maillet's work, as the number of authors who expressed views on the plurality of worlds around 1750 was immense. Historical treatises on pluralism aim at covering several aspects of the doctrine of plurality of worlds, and the issue of pre-Darwinian evolutionism is irrelevant in this discussion.

[166] See, for example, de Maillet's ideas on a "flying fish evolving into a bird" and his belief in *hommes marins* (chapter B.3) which are the most quoted passages of his evolutionary views; in several modern reviews of early evolutionary ideas the fish-bird transition is the only verbatim quotation of his work.

[167] Historians often stress the importance of early geological investigations on the emergence of a general awareness of great periods of time, correctly regarding this awareness as a precondition for the emergence of evolutionary thinking (Albritton 1980; Berry 1968; Burchfield 1998; Gohau 1990; Haber 1959a; Haber 1959c; Porter 1977). Although I basically agree with this interpretation – large parts of *Telliamed* do refer to geology - I stress the importance of the views on the awareness of vast interstellar space as a precondition for the views on geological time-scale; see also Gould (1987), who criticizes wrong dichotomies related to the emergence of the deep time concept. Although de Maillet is often mentioned in connection to the geological investigation, the aspect of a plurality of worlds-discussion implied in these geological views are, as far as I know, not adequately acknowledged. De Maillet's views on geology had several components of what later became known as the "gradualistic school" in geology, a concept that was one of the pre-conditions for the formulation of Charles Darwin's evolutionary ideas. I suppose that de Maillet's views on geological time are highly relevant, since the impact of *Telliamed* in natural sciences was enormous and diversified. Further studies are needed to assess the association between geological time and pluralism in other naturalists in 18th and early 19th century.

APPENDIX C – Historical aspects related to the use of convergence as a tool in biology

C.1 Introduction

Although the focus of the present thesis is the use of convergence as a tool (= convergence approach, see definition in chapter 3) in human evolution, with special consideration on hominoid interaction with water, a precondition for the present investigation is to understand how convergence approaches are used in other biological fields. In the preparations for a previous work on convergence approach (Bender 1999a), I planned to invest a few weeks to evaluate historical reviews of this topic before the proper analyses of hypotheses on early hominin evolution. However, after some years (from 1993 to 1999), I have learned that although uncountable researches on adaptation imply, and some explicitly state, the epistemological relevance of convergences in adaptive analyses, the historical development of this field has been sadly neglected. Not only is the history of the use of convergence as a tool poorly understood – I was further unable to find any analyses on the similarities and differences in convergence approaches in different biological disciplines. The only statements on this topic I could find were succinct historical sketches in the introduction of works on life forms in ecological publications and in an introductory chapters in Mark Ridley's book on comparative methods (Ridley 1983, 3-9) (see Appendix E).[168] Interestingly, investigators working within different research programs usually do not refer to a connection between these disciplines concerning a common use of convergences approaches. This apply to research carried out on the already mentioned comparative methods and life forms (and other attempts to classify organisms according to non-homologous traits), as well to the use of non-homologous patterns of similarity for the formulation of useful generalizations of biological phenomena, as for instance in the description of patterns of territoriality in birds and mammals, the classification of organisms as r/K selected, and in different hypotheses focusing on certain aspects of ontogenetic development – e.g., the division between nidicolous and nidifugous or between altricial and precocial organisms, just to mention few (see chapter 2 for references).

This chapter describes few episodes related to the historical development and modern use of convergence in adaptive analyses this topic. With "few" it is implied that the present review is not conceived as an exhaustive investigation of this topic. These events are chosen primarily,

[168] Other investigations of the "comparative methods" that I consulted explicitly avoid a historical review of the topic, as for instance by Harvey and Pagel – they mention the difficulty to review this topic and refer to Ridley's book (Harvey & Pagel 1991, 6).

as already noted above, to supply the basis for own investigations on the use of convergence as a tool in hypotheses on human evolution treated in chapter 3. The review can be used as well as a preliminary work for more in-depths investigations on convergence approaches in biology.

C.2 Three chosen historical aspects of the term convergence

C.2.1 "Twigs turning against each other": the emergence of the term convergence

Although evolutionary ideas were already known from the 18th century (see Appendix B), it was only after the publication of Darwin's *Origin of Species* that naturalists had to incorporate the evolutionary view, or at least to justify why the evolutionary perspective was inadequate (Bowler 1983; Bowler 1989; Junker 1998b, 851; Lefèvre 1984). In Germany, this process of assimilation of the Darwinian paradigm was at the same time characterized by the attempt of anatomists to distance themselves from the natural philosophical school. The *Zeitgeist* of early 19th century was increasingly hostile towards speculation and favourable toward empirical approaches and concise theoretical constructs. One important aspect in this debate was the different views on convergences. In opposition to most evolutionists prior to 1859, Darwin was fully aware that cetaceans and other aquatic mammals are secondary aquatic organisms, and recognized clearly that these organisms could not be regarded as ancestral to terrestrial mammals. Guided by this perspective, Darwin automatically excluded discrepant organisms[169] as bridging links in phylogenetic trees, and most[170] naturalists in the decades following the publication of his *Origin of Species* followed his lead. Instead of being perceived as paradoxical or as gaps between distantly related taxa, the functional affinity between such organisms became a crucial argument in Darwinian evolutionary theory. Convergent evolution – as demonstrated by distantly related aquatic or flying animals –

[169] I proposed this term to designate species difficult to place in a single logical category in pre-Darwinian zoological treatises. Discrepant organisms were, for example, ostriches, secondary aquatic vertebrates, bats, carnivore plants, flying and climbing fishes, snakes, eels, blindworms and polyps. These organisms were perceived as paradoxical because they exhibit features atypical for closely related species; rather, they were perceived as functionally related to distantly related creatures. In pre-Darwinian period, discrepant organisms were often used to bridge distantly related taxa within linear and hierarchical schemes in the Aristotelian chain of beings (Bender 1999a); see Appendix A.

[170] Single authors were still confused by discrepant organisms, as for instance Gustav Steinmann when he speculated about dolphins as descendants of *Ichthyosaurus*; Steinmann assimilated Lamarck's ideas uncritically (see Appendix D). A similar faux pas in the interpretation of superficial analogies as homologies was expressed by the Friedrich H. Dieterici (1821-1903), an influential German orientalist with insufficient knowledge of zoology. In his book *Der Darwinismus im zehnten und neunzehnten Jahrhundert,* he speculated on the possibility that camels descent from giraffes. When the ancestors of camels began to eat from the ground instead from the trees – they had continuously to bend down in the process – soft tissues moved from the belly to the back of the primeval camels (Dieterici 1878, 65).

became a phenomenon of high heuristic value and examples of convergent organisms were and still are used to illustrate the power of natural selection in shaping organismic form.

The geometric aspect implied in the word "convergence" in evolutionary biology was suggested by Carl Vogt (1817-1895) – a German zoologist and geologist living in Switzerland. In his *Vorlesungen über den Menschen* (Vogt 1863, vol. 1, 285), he described the phenomenon of species independently developing similar traits (quoted from the English translation, *Lectures on Man)*:

> The simian type parts in various directions; it first divides into two chief branches – monkey of the old, monkey of the new world – each of these main branches produces twigs which seem more and more to part from each other. But on arriving at perfection *the ends of the twigs turn again towards each other*, so that from the fundamentally distinct families of the gibbons, Macaci, and baboons are developed the three anthropoid apes, which, by a number of common characters stand considerably nearer each other than the groups of which they are the heads. (Vogt 1864, lecture XVI, 468, italics added)

Because Vogt described the phenomenon of convergence within an evolutionary framework, it attracted Darwin's attention. He referred to Vogt's views in *The Descent of Man*:

> It is, however, possible, though far from probable, that the early progenitors of man might at first have diverged much in character, until they became more unlike each other than are any existing races; but that subsequently, as suggested by Vogt, they converged in character. When man selects for the same object the offspring of two distinct species, he sometimes induces, as far as general appearance is concerned, a considerable amount of convergence. (Darwin 1871, vol. 1, 230)

After mentioning opinions on convergence in pigeons expressed by Hermann Engelhard von Nathusius and alleged convergence in apes' brains expressed by Louis-Pierre Gratiolet, Darwin concluded:

> If this conclusion, which rests almost exclusively on brain-characters, be admitted, we should have a case of convergence at least in external characters, for the anthropomorphous apes are certainly more like each other in many points than they are to other apes. All analogical resemblances, as of a whale to a fish, may indeed be said to be cases of convergence; but this term has never been applied to superficial and adaptive resemblances. (Darwin 1871, vol. 1, 230)

In the next paragraph, by describing the fallacy of Vogt's views, he formulate an argument which is still valid today: "It would be extremely rash in most cases to attribute to convergence close similarity in many points of structure in beings which had once been widely different" (Darwin 1871, vol. 1, 230-231). In fact, Vogt's ideas on convergent evolution of apes towards different human races imply the highly anthropocentric idea that all organisms are part of an evolutionary process aiming at "perfection". For several early advocates of the evolutionary idea,[171] the evolutionary process was perceived as an inexorable production of more complex and "progressive" forms towards a humanoid life-form.

In his *Origin of Species* (1859) Darwin supplied several examples of convergences, which he called "analogous variations"[172]: (a) the independent development of electric organs in fishes (1859, 192-193); (b) of luminous organs in distantly related insects (1859, 193); and (c) the "very curious contrivance of a mass of pollen-grains, borne on a foot-stalk with a sticky gland at the end" in distantly related plants like *Orchis* and *Asclepias* (1859, 193). In later editions, Darwin included the example of (d) convergent evolution of eyes in cephalopods and vertebrates (1872, 151-152); (e) the independent modification of air-breathing apparatus in different groups of crustaceans (1872, 152-153); and (f) the convergent evolution of hair-claspers in parasitic mites (*Acaridae*) (1872, 153).

Some years after the publication of *Origin*, the German pioneer of evolutionary ideas Ernst Haeckel (1834-1919) listed several cases of convergences in a largely modified edition of his book *Natürliche Schöpfungs-Geschichte* (1868), supplying a description of the term convergence that is indistinguishable from analogous explanations in modern textbooks (here quoted from the English edition, which is based on the 8th German edition of 1889):

> A series of important phenomena, which appear to stand opposed to those of divergence or separation, are those of so-called convergence or resemblance. For while divergent selection makes forms that are perfectly alike absolutely different in the end by adaptation to changed conditions of life and activity, convergent selection, on the other hand, makes forms which were originally altogether different become extremely alike by adaptation to similar conditions of existence and similar functions. The warm-blooded whales are genuine mammals, which

[171] See (Gould 1996) on early and modern anthropocentric concepts on progress and increasing complexity in evolutionary thinking. In a famous passage on the last two pages of his *Origin of Species* Darwin wrote: "And as natural selection works solely by and for the good of each being, all corporeal and mental endowments will tend to progress toward perfection" (Darwin 1859, 489-490); this specific statement contradicts his main views on this topic. About Darwin's contradictory concepts on perfection see (Gould 1996, 135-146).

[172] Darwin changed the expression "analogous variations" with "all favourable variations" in the 6th edition (Darwin 1872, 152); see chapter C.2.2 for the reason for this change.

> have assumed the form of fish by having adapted themselves to their mode of life; but they are descended from land mammals, and, moreover, the herbivorous Sirenia, probably from hoofed animals, the carnivorous dolphins and bearded whales from rapacious animals. In these two groups, convergent selection has not only changed the external form; the inner structure too has become so alike, that they were formerly classed as one order. (Haeckel 1876, 314-315)

After Haeckel included the extinct aquatic reptile *Ichthyosaurus* as convergent to cetaceans in later editions (Haeckel 1909b, vol. 1, 272), the tradition of using these animals as examples of convergences was initiated and became an inherent part of biological textbooks for the next hundred years.

C.2.2 The interpretation of convergences in the framework of orthogenetic ideas

Beside the establishment of convergent organisms as textbook's examples to illustrate the power of natural selection, several authors were inclined to see the phenomenon convergence from a completely different perspective. It is useful to analyze some of these views in influential textbooks published after 1859, as for example in the works by Carl Gegenbaur (1826-1903). The first edition of his *Grundzüge der vergleichenden Anatomie* (Gegenbaur 1859) was evidently not influenced by Darwin's evolutionary ideas, as it was published in the same year as the *Origin of Species*. Gegenbaur divided the organisms into components, describing certain organs in a sequence that reflected the authors' opinion of an ascending scale of complexity in different groups of organisms. Gegenbaur's comparative anatomy is a good example of how scientists in the second half of the 19th century were able to transform typological views in evolutionary thinking. The language used was often the same - German expressions like *Bauplan* (body plan), *Typus* (type), *Urtypus* (archaic or archetypical type), *Grundform* (basic form) could be used both by essentialistic and non-essentialistic thinkers.[173] However, Gegenbaur's use of the concept of types was formulated in a way that suggested the influence of idealistic philosophy.

Gegenbaur differed in two aspects from most of his predecessors in comparative anatomy. Firstly, he opposed the concepts homology and analogy (Gegenbaur 1859, 35-36), terms explicitly defined by Richard Owen as follows: homology – "same organ in different animals

[173] After the increasing rejection of idealistic ideas in biology, essentialistic concepts were changed to accommodate non-idealistic concepts in systematics, or transformed to hide idealistic views (on essentialism see Appendix D). See for instance the ideas defended by the German botanist Wilhelm Troll (1897-1978) and the German pathologist Max Westenhöfer, who were both influenced by Goethe's idealistic morphology (Bender-Oser 2004a, 54-77); see Appendix F). Adolf Remane, an influential German zoologist, who published several articles against essentialistic ideas in biology (see Appendix D), discussed also the problem of *Typus* in morphological biology (Remane 1951a).

under every variety of form and function" (Owen 1843, 379); analogy – "part or organ in one animal which has the same function as another part or organ in a different animal" (Owen 1843, 374); see Rupke (1995). Secondly, in the first edition of this work there is a recognizable incipient attempt to integrate embryological research in anatomical comparative studies to clarify relationships between organisms. This approach was further developed in the second edition of this work published eleven years later, which then also integrated Darwin's evolutionary concepts. By doing so, Gegenbaur influenced several prominent naturalists and evolutionists, as for instance the German evolutionist Ernst Haeckel.

Gegenbaur clearly formulated the main goal for what later became the traditional research programme in comparative anatomy: the identification and description of homologies to understand natural relationships between the treated groups (Gegenbaur 1859, 35; 1874, v). He was convinced that homologies are much more relevant for comparative studies than analogies: while the first are identifiable in the *Bauplan* of a restricted number of organisms conditioned to a certain *Typus*, the latter are based only on the functional similarity between organs and "can be regularly found in the whole animal kingdom (*Thierreich*), since a certain amount of functions has to be provided in each animal" (Gegenbaur 1859, 35, my translation). Within the Darwinian paradigm, the concept of organisms belonging to a *Bauplan* became intrinsically connected with the concept of organisms sharing traits due to a common ancestry. Before the emergence of genetic analysis, comparative anatomy (complemented by palaeontological and later ethological research) became the most reliable way to place every organism in the right systematic position.

The study of analogy had a very different historical development to the study of homology. As we will see, the adaptive similarity between organisms had long been regarded as impressive and insightful. However, for the purpose of systematics they were often considered as completely irrelevant or even an obstacle. In fact, convergences between organisms have to be identified and excluded from analysis of genealogical relationships between organisms, and are therefore often perceived as mere "noises" which hampered the study of homology. With the increasing status of systematics in evolutionary biology, the heuristic value of convergences was sporadically appreciated by single researchers working in different biological fields (for explanations and references see chapter C.4).

A further negative connotation of the term convergence is related to the fact that functional similarities between distantly related organisms were often used by early naturalists in orthogenetic concepts. The term orthogenesis was first proposed by Wilhelm Haacke in his

book *Gestaltung und Vererbung* (Haacke 1893). In a discussion on preformationism and epigenetics he wrote:

> The evolution within each lineage [*Abstammungslinie*] took place only in one direction. The mammals derived perhaps from amphibians, and these from primitive forms of fishes […], but never and nowhere was a mammal transformed back into an amphibian, or an amphibian transformed back into a fish. (Haacke 1893, 32, my translation)

Starting from this argument, Haacke inferred that the evolution of organisms is characterized by unilinear and unidirectional tendencies. These constrains are, so Haacke argued, the result of the limited capacity of germ plasm to produce arbitrary variations. Proponents of orthogenesis had different, often contradictory views (see Delage 1903, 470-481). Generally, they argued that the development of certain organs and structures are directed, since they follow certain predetermined pathways. These predetermined pathways, so was argued, often led to maladaptive features, and were sometimes responsible for the extinction of species (see Bowler 1983, 141-181; 1996, 67-74). Proponents of orthogenesis were sceptical about the Darwinian view of organismic diversity as being produced by random mutations and natural selection. It seems paradoxical that convergent evolution – already perceived as an example of the power of natural selection in the production of adaptive features by earliest Darwinians – was also used by orthogeneticists to illustrate the power of "internal forces" to produce organismic diversity. One example of an evolutionary theory based on orthogenesis was proposed by the Russian zoologist and geographer Leo Semyonovich Berg (1876-1950) in his book *Nomogenez ill evoliutciia na osnove zakonomernostei,* first published in Russian in 1922 and translated into English in 1926 with the title *Nomogenesis or Evolution Determined by Law* (here quoted from the second edition from 1969). As other proponents of orthogenetic ideas, Berg believed that evolution is not a random process, and he used the phenomenon of convergence to underline this assumption. Berg quoted the following passage of Darwin's *Origin of Species*, where he proposed an analogy between human inventions and the development of organismic features to explain the emergence of convergences:

> In all these cases of two very distinct species furnished with apparently the same anomalous organ, it should be observed that, although the general appearance and function of the organ may be the same, yet some fundamental difference can generally be detected. I am inclined to believe that in nearly the same way as two men have sometimes independently hit on the very same invention, so natural selection, working for the good of each being and taking advantage of analogous variations, has sometimes modified in very nearly the same manner two parts in

> two organic beings, which owe but little of their structure in common to inheritance from the same ancestor. (Darwin 1859, 193-194)

Later Darwin seemed to recognize that the expression "analogous variations" in the extract above was imprecise and ambiguous, since it could be interpreted as suggesting variations between two convergent species that arose as exact copies "already" analogue to each other – a highly improbable process which implies an evolutionary process guided by orthogenetic driving forces. In fact, such an interpretation is diametrically opposite to what Darwin wrote in the two first chapters of his *Origin of Species.* Darwin's theory of natural selection did not admit anticipation of the future. Probably for this reason Darwin changed the expression "analogous variations" with "all favourable variations" in the 6th edition (Darwin 1872, 152). This formulation mitigated the danger of misinterpretation of the concept of natural selection, since it now implies that convergences arise not due to analogous variation, but to contingent variation supplying the raw material for the operative effect of natural selection.

Berg was aware on Darwin's changes in the quotation above. Nevertheless, in his attempt to prove the existence of orthogenetic tendencies in the evolution of organisms, Berg exploited the ambivalence of Darwin's original expression by showing the improbability of variations arising by chance to fulfil the preconditions required for convergent organisms. He wrote:

> Since every useful variation according to Darwin's theory arises by chance, it is scarcely credible that such a variation should arise accidentally even in one species; but still more incredible would be its occurrence in different species having no common ancestors. Natural selection is powerless to effect anything, if the probability of the occurrence of a certain character may be approximately zero; unless, as it has been tacitly assumed in the passage cited above, the same functions be attributed to natural selection as are attributed to vital force. (Berg 1969, 158)

An obvious problem with Berg's arguments is his erroneous assumption that variations had to be exactly the same in two convergent species. The fact that convergences in two distantly related species are not necessarily based on the same morphological construction is especially evident in convergences between the European mole cricket (*Gryllotalpa gryllotalpa*) and mole (*Talpa europea*), or between hummingbirds (Trochilidae) and moths of the family Sphingidae, such as the hummingbird hawk moth (*Macroglossum stellatarum*).

The use of convergences to challenge the power of natural selection is a standard argument of anti-Darwinists – or opponents of the Darwinian concept of natural selection or from

biologists attempting to justify the use of religious instinct in scientific investigations.[174] In a paper on convergence, Richard Hesse emphasized the physical and chemical nature of biological phenomena. By addressing his criticism specifically against Berg's arguments, Hesse vehemently rejected any attempt to interpret convergences as the product of orthogenetic tendencies. For him the belief of "an immanent purposefulness" [*immanente Zweckmässigkeit*] in the evolution of convergences is a cheap excuse, which "just covered up [*bemäntelt*] our ignorance" (Hesse 1939, 13).

C.2.3 The definitive establishment of the modern convergence concept after the rejection of orthogenetic views

The gradual rejection of orthogenetic ideas was an important aspect of the establishment of the synthetic evolutionary theory (Junker 2004). One enlightening example of interpreting convergences in a framework hostile to natural selection among German speaking scientists can be found in works by the German zoologist and evolutionist Bernhard Rensch (1900-1990). Before he changed his mind and became an important German pioneer of the synthetic evolutionary theory, he defended Lamarckian and orthogenetic views of evolution in the late 1920s and early 1930s. Early in his career, Rensch carried out research on the dependence of several avian features (like body size, proportions of legs, wings, bill, and colors of the plumage) on climatic conditions. For instance, he interpreted certain convergences among birds from a "Lamarckian point of view" [*im lamarckistischen Sinne*] or as orthogenetic predetermined coerciveness, "which contradict the Darwinian implication of contingency" (*Zufallsprinzip*) (Rensch 1923, 32). He summarized his results in his first book published in 1929 on speciation, where he defended the opinion that the climatic parallelism of race formation could be explained by a direct influence of the environment on inherited characters. His view was influenced by the fact that mutations of birds analyzed by ornithologists concerned larger differences, while the differences between neighbouring races, running parallel to climatic changes were rather insignificant. He thought, therefore, that climatic selection was probably not responsible for such insignificant differences (Rensch 1929).

According to Rensch himself, he gave up all Lamarckian explanations in early 1930s when geneticists showed that "nearly all genes have pleiotropic effects and that selection can become effective during some thousands of generations even when the advantage of a new

[174] For examples of the use of analogy in attempts to undermine Darwinian views by creationists see MacKenzie et al. (2004)and Price (1925). There are several indications that one of the few works published in recent years (Conway Morris 2008) focusing on the phenomenon convergence was motivated by similar religious feelings (see also chapter C.5.1), although not reaching the same anti-Darwinian conclusions as the authors quoted above.

allele is only 1 to 2 percent" (Rensch 1980, 296). He then began to explain climatic parallelism of racial differences in several features by natural selection, for instance concerning (a) parallelism in birds and mammals (Rensch 1936), (b) parallelism in land snails (Rensch 1937) and (c) climatic rules on homeothermic animals (Rensch 1938).[175] In his book *Neuere Probleme der Abstammungslehre* (first ed. 1947, second ed. 1954, translated into English and published in 1959 as *Evolution Above the Species Level*), an important work for the consolidation of the synthetic theory of evolution in German-speaking countries, Rensch underlined his views on the development of parallel forms as the product of undirected mutation and natural selection, stressing the role of pleiotropic genes and ontogenetic allometric parallelism (Rensch 1972, 182-183). By denying any role of "special autonomous development forces" (Rensch 1972, 215) in the manifold cases of parallelisms and convergences, he defended still valid views on these topics.[176]

C.3 Early attempts to consider comparative anatomy from a broader perspective: Carl G. L. C. Bergmann and Rudolf K.G.F. Leuckart

Several early authors, even some working in pre-Darwinian period, pointed out to what they believed to be a negative focus of biological investigation, in which homology was emphasized at the cost of research on analogy. It is interesting that these authors aimed a perspective which takes into account the complex relationship between organisms and their environment. The difference in approach is very well illustrated throughout the book on comparative anatomy *Anatomisch-physiologische Übersicht des Thierreiches* (Anatomic-physiological overview of the animal kingdom) written by the German authors Carl G.L.C. Bergmann (1814-1865) and Rudolf K.G.F. Leuckart (1822-1898) (1855, first publ. 1852). As an anatomist and physiologist, Bergmann is known to modern biologists because of his famous ecogeographic principle (see below); Leuckart is one of the most distinguished zoologists of the 19th century. In their book these authors presented zoological knowledge from a physiological point of view, stressing the function of different parts of organisms - anatomical descriptions were only considered when necessary to understand physiological factors. The authors made great efforts to present organisms in a broader perspective than in other anatomical books, stressing a comparative approach by considering each organism's mode of life. This approach is supported by the concept of the book, which divergent from

[175] On Rensch's role on the synthetic theory of evolution and his earlier views on mechanisms of evolution see (Bender 1999b, 80-81; Junker 2004, 308-309; Mayr 1980; Rensch 1980).
[176] See however Gould (2002, 352), who aptly criticizes an on-sided view negative evaluation of all ideas concerning orthogenesis.

most contemporaneous (and modern) textbooks by its treatment of both vertebrates and insects (Bergmann was primarily responsible for the text on vertebrates, Leuckart for the text on insects.) Most insightful were the comparative notes on the different locomotory systems, especially from vertebrates (pp. 398-404), the discussion on "dermal formations" [*Hautgebilde*] from vertebrates in relation to movement (pp. 404-412); and the comments on pneumatic organs in several taxa, for instance, the functional meaning of the pneumatisation of bird's bones or the physiology of the swim bladder in fishes (pp. 412-426). In all these chapters the authors treated anatomical evidence in a broad context, with references to the environment in which the organisms live and with constant references to convergent solutions in distantly related organisms.

The interest for convergent evolution can be found in other works of both authors. For instance, one year before the first edition of *Über das Verhältnis*…, Leuckart published an interesting work entitled *Über den Polymorphismus der Individuen oder die Erscheinung der Arbeitsteilung in der Natur* (1851) (On the polymorphism of individuals or the phenomenon of division of labour in nature) in which he addressed the problem of divergent phenotypes in panmictic populations. The topic is especially important in evolutionary biology due to the commonality of this phenomenon in several taxa and the implication for research, for instance, in discussions on niche diversity, on mimicry, or on the phenomenon of social polymorphism in social insects. Leuckart's publication is regarded today as the basis for all subsequent investigations on this topic, insofar as they do not concern genetic or cytological research (see, e.g., Schmidt 1987, 2).

Naturalists interested in closely related organisms living in different environments were prone to search for patterns of convergences between these organisms and include them in analyses on adaptive features. Bergmann's interest in convergent patterns led to the formulation of the ecogeographic principle called "Bergmann's rule". In its original form, this rule applies to geographic variation, predicting an inverse correlation between temperature and mean body size in endothermic animals as an energetic adaptation to colder regions (Bergmann 1847). In fact, the search for non-homologous patterns of similarity to formulate predictions on the adaptive characters of organisms had been carried out already by earlier authors. For instance, inspired by an earlier work[177], the German zoologist and ornithologist Constantin L. Gloger (1803-1863) observed that birds tend to be heavily pigmented when living in more humid

[177] By 1811, the German naturalist Peter Simon Pallas (1741-1811) had already pointed out that patterns of colouration in birds varied according to environmental conditions (Pallas 1811), a work that Gloger dully acknowledged.

environments than their relatives living in more arid environments (Gloger 1833); see Burtt and Ichida (2004) and Tiquia et al. (2005) for a possible explanation of the Gloger's rule.

These early authors were the forerunners of evolutionary works stressing the value of convergent organisms in the analysis of adaptive features after 1859.

C.4 Convergence: role in merging research on animal geography with ecological research

In the second half of the 19th century and especially in the first half of the 20th century, some important concepts relating to convergent evolution were formulated within a discussion on ecogeographic regularities. In some cases, the framework in which these concepts were developed was influenced by the tradition established by Carl Bergmann and his predecessors, which is evident in the research carried out by the American zoologist Joel A. Allen (1877), by the German zoologist Richard Hesse (1924) and by the German evolutionary biologist Bernhard Rensch (1936; 1938; 1950). From today's point of view, it may sound superfluous to indicate that a zoological work should stress the environmental aspects of animals. However, the perspectives of the late 19th and early 20th century were completely different from modern research programmes. By 1884, the Scottish biologist Patrick Geddes (1854-1932) had already criticized an excessive focus on the descriptive approach used in classical comparative anatomy, and argued for a more interdisciplinary approach focusing on the organism as an intrinsic part of the environment in which it lives (Geddes, quoted in Böker 1935, 3).[178] The physiologists Walter Stempell and Albert Koch criticised that the zoological training in most German universities in early 20th century focused on systematics and morphological studies, ignoring other crucial aspects of biological research (Stempell & Koch 1923). The physiologist Albrecht Bethe (1872-1954) observed with biting sarcasm that zoologists became so absorbed in morphological details that they seem to have forgotten that they were dealing with living organisms (Bethe 1917).

The German zoologists Richard Hesse (1868-1944) and Franz Theodor Doflein (1873-1924) argued in a similar way in their zoological work entitled *Tierbau und Tierleben: In Ihrem Zusammenhang betrachtet* (Animal form and life considered as a whole), published in two volumes (Hesse & Doflein 1910; Hesse & Doflein 1914). They complained that after the

[178] See also the book *Life: Outlines of General Biology* Geddes' by the Scottish biologist John Arthur Thomson (1861-1933) and Geddes. In this work, the authors illustrate "with more care, and in more detail, than usual, the relations between Biology and other Sciences" (Thomson & Geddes 1931, vol. I, v), stressing the need of ecological analyses (1931, vol. I, v, 42-225).

establishment of Darwin's evolutionary theory, most zoologists invested their energy almost entirely on morphological disciplines and systematics, neglecting so the biological[179] view of organisms (Hesse & Doflein 1910, vii). Impressive through the enormous amount of zoological data, *Tierbau und Tierleben* is among the first broadly conceived zoological works presenting comparative morphological analyses with consideration of the intrinsic relationship between organisms and their environment. Popular among biologists at the time,[180] *Tierbau und Tierleben* had a considerable influence on German speaking naturalists of this era, stimulating research focusing on the limitation and the potential of adaptive characters and driving a new focus on investigations of convergent adaptations. Although it was not basically a work on experimental physiology, it had also a strong impact in the development of this discipline.

Hesse and Doflein were crucially influenced by the above described work of Bergmann and Leuckart; Hesse and Doflein considered it as the first zoological book which aimed at a biological perspective, and deplored that this book was almost forgotten by contemporaneous young zoologists. They expressed their admiration of Bergmann and Leuckart by dedicating their first volume to these authors (Hesse & Doflein 1910, vii). In their attempt to stress the importance in studying organisms as interactive and coordinated parts of a living system, Hesse and Doflein followed[181] the idea formulated by the German anatomist and embryologist Wilhelm Roux in his work *Der Kampf der Theile im Organismus* (The battle of parts in the organism) (Roux 1881) which was well received by naturalists at the time, such as Darwin and Haeckel (Gould 2002, 210-213; Mocek 2001). Roux had made an analogy between Darwin's "struggle for life" between species or between individuals of the same species, and a "struggle for life" between parts in the same organism. According to this view, cells, tissues or organs are concurrent with other parts of the organism for space or nutriment, and changes in one feature have consequences on other features in the same organism.[182] Other influences on the strong emphasis that Hesse and Doflein gave to environmental aspects of organismal adaptations came from their familiarity with ecological concepts formulated by

[179] The expression "biological" was often used in this time in the sense of "ecological", see also below Böker's "biological anatomy". Also the expression "physiological" was often used in the same sense, as Friedrich Dahl (1921, part ii, 1) interpreted the word when commenting on Andreas F.W. Schimper's book *Pflanzengeographie auf physiologischer Grundlage* (1898).

[180] The German physician, anthropologist and eugenicist Eugen Fischer (1874-1967) described it as well known and indispensable for every general biologist and zoologist (Fischer 1944).

[181] The similarity between Hesse's/Doflein's and Roux's ideas is not accidental: Hesse and Doflein knew Roux's work (Hesse & Doflein 1910, 765-766; Hesse & Doflein 1914, 917).

[182] Roux's arguments have similarities with Cuvier's argument of correlations of parts (see above), which is succinctly mentioned in the introductory part of the book (Roux 1881, 12).

the German zoologist Karl August Möbius (1825-1908) in his seminal work *Die Auster und die Austernwirtschaft* (Oyster and oyster farming) (Möbius 1877).

This influence was everything else than casual. Möbius' formulation of the concept of biocenosis and his research on this topic had a strong impact on biology at this time, leading to the formulation of the research programmes of ecology and marine biology (see Glaubrecht 2008). As one of the consequences of his research, several works on animal and plant geography in late 19th and early 20th century were published with the specific goal of including ecological perspectives in zoogeographic research.[183] For instance, Hesse published a research programme in the article *Die ökologische Grundlagen der Tierverbreitung* (1913) and planned its realization in a book with the title *Ökologie der Tiergeographie* (Hesse 1924, v). However, shortly before the book was finished, Friedrich Dahl - a former student of Möbius and later his assistant (Buschbaum et al. 2003; Leps 2001) - published a book entitled *Grundlagen einer ökologischen Tiergeographie* (Dahl 1921). Owing to the great similarity of titles, Hesse changed the title of his own work to *Tiergeographie auf ökologischer Grundlage* (Hesse 1924).[184] As intellectual adversaries, both authors were suspicious about the approach used by the other. Dahl mentioned Hesse's work in a second volume of his *Grundlagen einer ökologischen Tiergeographie*. He criticized Hesse's article on ecological zoogeography for its consideration of internal and external anatomy in a zoogeographic investigation (Dahl 1923, 1-2). Hesse, in turn, regarded Dahl's book as not a work on ecological zoogeography, at least not what he understood to be this term (Hesse 1924, v). In fact, the reciprocal criticism reflected not only the competition between two leading researchers, but also a problem still discussed today – the multi-disciplinary nature of biogeography that lead to difficulties in identifying the boundaries between biogeography and overlapping fields like ecology, evolutionary biology or palaeontology (MacDonald 2003; Müller 1977, 16). Hesse was interested in a broader interpretation of zoogeography, with a strong inclusion of morphological knowledge. In this sense, Hesse's "morphological zoogeography" had similarities with today's ecomorphology and with the approaches proposed by Othenio Abel and Hans Böker (see chapter 2 for references). Hesse's work is also characterized by the

[183] Möbius himself wrote an article on the influence of food on the dissemination and migration of animals entitled *Über den Einfluss der Nahrung auf die Verbreitung und die Wanderung der Thiere* (On the influence of food on the proliferation and the migration of animals) (Möbius 1881). This almost unknown work – I found it only quoted in a small zoogeographic book (Maas 1907), and an internet research shows only hits from a couple of digitalized contemporaneous publications - was based on a talk that Möbius gave in the geographic society in Bremen.

[184] According to Hesse (1924, v), the title was inspired by Andreas F.W. Schimper's *Pflanzengeographie auf physiologischer Grundlage* (1898), a book which always served as model for him. Hesse's book had a rewritten edition in English in 1937 [*Ecological animal geography*].

attempt to classify organisms according to functional groups. This is, for example, evident is his broad classification of animals taking in consideration the circumambient medium in which these organisms live: he distinguished between *Wassertiere* (aquatic animals, divided in primary and secondary aquatic animals) and *Lufttiere* ("air animals", not meaning flying but air-breathing animals) – these were sub-divided in *Feuchtlufttiere* ("moist air-animals") and *Trockenlandtiere* ("dry air-animals") (Hesse 1924, 27-50).[185] See also chapter C.2.2 on Hesse's contribution to the research stressing intrinsic relationship between organisms and their environment, and his criticism towards orthogenetic views concerning convergences.

Returning to *Tierbau und Tierleben,* in several chapters of this work, Hesse and Doflein discussed organic systems in distantly related organisms, choosing topics which allow a broad comparative perspective between different taxa, for instance hemophagic adaptations or animal migration. Hesse, in particular, was very interested in convergence between distantly related organisms. Owing to his broad and in-depth knowledge on adaptive forms, he was able to give several examples of convergences to discuss different aspects of ecology and evolutionary concepts and to demonstrate the potential and limits of adaptation to a broad spectrum of environmental conditions. He discussed, among others, (a) convergences in the origin of land snails (pp. 41-42); (b) convergent adaptations to arid regions (p. 45); (c) adaptive convergences between marsupials and placental mammals (p. 74); and (d) between not-closely related birds (pp. 74-75); (e) convergent development of chisel-shaped incisors to a blade-shaped set of teeth (as found in the Osteichthyes of the genera *Balistes*, *Ostracion* and *Diodon* (p. 229)); (f) convergences in buoyancy structures of pelagic organisms - mentioning in the same context radiolarian, the basking shark (*Cetorhinus maximus*) and ocean sunfish (*Mola mola*) (p. 235).

Hesse's interest in convergences is also evident in other publications. In an article dedicated entirely to this topic entitled *Konvergenz* (Hesse 1939) he stated that convergences are "probably among the central issues [*Hauptprobleme*] in ecology" (Hesse 1939, 3). However, he recognized the difficulties in any attempt to classify convergences. He stated that the development of similar biological traits in unrelated lineages sometimes concern extensive resemblances between organisms – for instance the remarkable similarities between the common pill-bug (*Armadillidium vulgare*) and pill millipede (*Glomeris marginata*), both able to roll up into a ball when disturbed. Other convergences, he wrote, concern only certain

[185] Curiously, this classification is remarkably similar to the views expressed by the Roman naturalist and philosopher Pliny the Elder (23 AD-79 AD), who in his *Naturalis Historia* distinguished between terrestrial and aquatic animals (Caius Plinius Secundus 2007, vol. I, 441-523).

aspects of organismal features such as the wings of birds and bats, without major resemblances in other structures. However, a clear distinction between extensive and partial convergence is not possible, given the several examples of graduations between the two categories. For Hesse, it was more reasonable to distinguish between adaptive (*sinnvolle*, or useful) and non-adaptive (*sinnlose*, or useless) convergences. In his opinion, the great majority of convergences are adaptive[186] (*Anpassungskonvergenzen* = adaptive convergences); he gave among others the following examples for "adaptive convergences": (a) the aestivation of organisms living in moss mats on rocks or tree trunks, which are exposed to regular events of desiccation and rehydration; (b) the degeneration of functional wings in several insect groups living on Antarctic islands and regularly exposed to strong winds; (c) the regressive evolution of eyes and other convergent features in cavernicolous organisms[187]; (d) the regressive evolution in several parasitic organisms; and (e) convergences of marine organisms from different taxa living on the sandy bottom of shallow seas, which are characterized by small body size (less than 2mm).[188]

All these observations on convergences are based on the same procedure: on the one hand, the identification of divergent adaptive patterns across species or across variations of the same species; and on the other hand, the identification of similar patterns in distantly related species. The same approach is implied in the several attempts to classify plants and animals according to non-homologous patterns of similarity from their external morphology, which is reviewed in the next section.

C.5 Attempts to classify living organisms in non-phylogenetic groups

In addition to the Linnaean classification of animals and plants based on the most conspicuous differential characters of each taxon, some pre-Darwinian naturalists tried to classify organisms according to non-phylogenetic criteria, as for instance taking into consideration similar behavioural, physiological or anatomical adaptations to their environment.

C.5.1 Two "comparative approaches" in 18th century: Duncan and Gregory

Before we analyse the more scientific treatises on this topic, let us see one examples how a thinker in early 19th century presented a synopsis of organisms according to different criteria,

[186] As examples of "useless convergences" he mentioned the convergent patterns in the shell shape of scallops (Pectinidae), without further theoretical corroboration of his view; see empirical work by Serb et al. (2011) on the possible adaptive value of shell shape in Pectinidae.
[187] For investigations on this topic see (Dowling et al. 2002; Parzefall 1984; Schemmel 1984; Wilkens 2010)
[188] Later, Adolf Remane (1951b; 1934) carried out this research in connection with life forms of shore organisms; see also chapter C.5.2.

and how a physician in 18th century used a comparative approach in his speculations of human mental abilities and other issues.

The first example concerns remarkable, but widely ignored work by John Shute Duncan (1768-1844) entitles *Analogies of Different Classes of Organized Beings* (Duncan 1831); Duncan was keeper of the Ashmolean Museum at Oxford between 1823 and 1829.[189] In the introduction of this work, Duncan explained that he was interested in genera and species which strongly diverge and at the same time "may possess analogical agreement amongst themselves scarcely less clear, and at least equally deserving our attention" (Duncan 1831, 1).

Duncan tried to organize several organisms in a "table of analogies", in which the subjects selected and named at the head of each of the columns have been chosen for a synoptic presentation of analogies between different classes of animals and plants. Duncan's table of analogies was arranged according to different criteria, for instance taking in consideration the environment of mammals (*Land*: "Lion, Dog, Bull, &c." / *Land and Water*: Otter, Hippopotamus / *Water*: Dugong, Whale) or some of their anatomical features, e.g., "Feet" (*Armed to lacerate*: Lion, Wolf / *Contra*: Edentate, Sloth, Ruminantia, Cow, Sheep) or – as a concession to the anthropocentric view of nature popular in this time - according to their "Benefit or injury to Man"(*Benefit*: "Herbivora, generally" /*Injury*: "Some Rodentia. Carnivora, Dog & Cat excepted") (Duncan 1831, 10-18). Although Duncan mentioned that "animals and plants of all classes exhibit peculiar adaptations to each condition of temperature" (Duncan 1831, 4), his treatise cannot be regarded as a precursor to evolutionary ideas. In fact, Duncan follows both scientific and religious purposes– a common procedure in this time, as is evident for instance in his physico-theological arguments; on physico-theology (or natural theology) see Appendix B, chapter B.4.3. Duncan is explicit in his belief that "in analogies we chiefly trace the unity of the designing Cause" (Duncan 1831, 4) and in his positive remarks on the work of natural theology by the English geologist, palaeontologist and theologian William Daniel Conybeare (1787-1857), in which the author writes on the natural evidence to prove the existence of an intelligent designer of the universe using, among others, arguments from analogy (Conybeare 1831, 58-85). Although statements on analogy of

[189] John Duncan was succeeded in 1829 by his brother Philip Bury Duncan. On their activities in the museum see the website "British Archaeology at the Ashmolean Museum" the article *History of the British Collections: The Nineteenth Century* in **(**http://britisharchaeology.ashmus.ox.ac.uk/collections/history-19thcentury.html**),** retrieved on 7 January 2014**.**

organisms following both theological and scientific purposes are almost absent in modern evolutionary debate, this is only true for peer-reviewed publications.[190]

Our second example concerns a similarly ignored booklet entitled *A Comparative View of the State and Faculties of Man with Those of the Animal World* written by the Scottish physician and moralist John Gregory (1724-1773). It was published first anonymously in 1765 and had several editions under Gregory's own name; it was also translated in German and in French; it is quoted here from the 4th edition from 1767. Concerning his comparison between humans and other animals, Gregory basically disagreed with the general view of man "as a Being that had no analogy to the rest of the Animal Creation" (Gregory 1767, 7). He argued that although several investigations on comparative anatomy of (non-human) animals had been carried out, "the comparative Animal Oeconomy of Mankind and other Animals, and comparative Views of their states and manner of life, have been little regarded" (Gregory 1767, 7). Rather unusual for this time, he explicitly stated that the closeness of humans to other animals would be a source of discomfort to humans:

> The pride of Man is alarmed, in this case, with too close a comparison, and dignity of philosophy will not easily stoop to receive a lesson from the instinct of Brutes. But this conduct is very weak and foolish. Nature is a whole, made up of parts, which, tho' distinct, are intimately connected with one another. This connection is so close, that one species often runs into another so imperceptibly, that it is difficult to say where the one begins and the other ends. This is particularly the case with the lowest of one species, and the highest of that immediately below it. (Gregory 1767, 7-8)

He used an interesting logic in his attempt to understand living organisms, based on their place in the *scala naturae*:

> On this account no one part of the great chain can be perfectly understood, without the knowledge, at least, of the links that are nearest to it. In comparing the different species of

[190] For instance, in the book *Life's Solution: Inevitable Humans in a Lonely Universe* (2008) the English palaeontologist and Christian Simon Conway Morris uses the phenomenon of convergence to underline his claim that "adaptation is not some occasional cog in the organic machine" (Conway Morris 2008, xv), an assumption which is intrinsically related to his religious beliefs. For instance, in the chapter "Towards a theology of evolution?" he claims that "it is reasonable to take the claims of theology seriously" (Conway Morris 2008, 328) and that "salient facts of evolution are congruent with a Creation" (Conway Morris 2008, 329). Similar statements can be found in some contributions of the book *The Deep Structure of Biology: Is Convergence Sufficiently Ubiquitous to Give a Directional Signal?*, (Deane-Drummond 2008; Haught 2008), a work edited by Conway Morris. See also Conway Morris' interview on the website of The Faraday Institute for Science and Religion (Conway Morris 2012). Conway Morris' interest in convergences is also evident in the website "Map of Life" (www.mapoflife.org), a project sponsored by the John Temple Foundation which documents several examples of convergences. For a criticism of Conway Morris' views on convergence see (Powell 2007) and several blogs in the internet.

> Animals, we find each of them possessed of powers and faculties peculiar to themselves, and well adapted to their particular sphere of action which Providence has allotted them. But, amidst that infinite variety which distinguishes each species, we find many qualities in which they are all similar, and some which they have in common. Man is evidently at the head of the Animal Creation. He seems not only to be possest of every source of pleasure, which any of them enjoy, but of many others, to which they are altogether strangers. If he is not the only Animal possest of reason, he has it in a degree so greatly superior, as admits of no comparison. (Gregory 1767, 8-9)

However, despite the promising title, it is evident that Gregory used a comparative approach particularly to introduce medical and philosophical issues in a broad context. For instance, before he began to discuss the causes of high mortality in children (Gregory 1767, 18-63), he succinctly mentioned what he believed to be the most crucial aspect of this topic:

> By the most accurate calculation, one half of Mankind die under eight years of age. As this mortality is greatest among the most luxurious part of Mankind, and gradually decreases in proportion as the diet becomes simpler, the exercise more frequent, and the general method of living more hardy, and as it doth not take place among wild Animals, the general foundations of it are sufficiently pointed out. (Gregory 1767, 20)

These and other aspects of Gregory work makes him interesting for historical investigations on the establishment of medical ethics (see, e.g., McCullough 1998).

C.5.2 Life-forms and related concepts

There were several attempts to classify organisms according to functional features proposed by researchers interested in the adaptive features related to environmental conditions, often in the framework of ecological research and related fields. By focusing on different features and different aspects of the environment, these classifications had different results. Contrary to the Linnean classification, these attempts were not part of an organized research programme, but were often the product of the work of single investigators, without a pronounced tradition within biology.

Some attempts to classify plants according to plant function in the ecosystem are known by the term “growth-forms” or “life-forms”. These concepts take non-homologous patterns of similarity from the external morphology of plants as the basis of the classification. Some concepts on plant-physiognomy (and this term) were later published by Alexander von

Humboldt (1806),[191] followed among others by Anton Kerner von Marilaun (1869), August Griesebach (1872) and Eugenius Warming (1895). The latter author proposed the term "life-forms", which was then translated in English as "growth-forms".[192] The Danish botanist and pioneer of plant ecology Christen C. Raunkiaer (1860-1938) proposed the term "life-forms" at the beginning of the 20th century (see Tansley in Raunkiaer 1934, xi-xvi). He envisaged a system of classification of plants based on the protection afforded to the perennating buds (or shoot-apices) by their position in relation to the surface of the soil during the unfavourable season to plant life. He originally proposed the division of five groups of plants: phanerophytes, chamaephytes, hemicryptophytes, cryptophytes, and therophytes (Raunkiaer 1934). Raunkier's system is certainly the most widely applied categorization of life-forms in plants; his system was extended by other authors, such as Ellenberg and Mueller-Dombois (1966) and D.W. Shimwell (1971).

The Austrian botanist Helmut Gams (1893-1976) included animals in the analysis of life-forms in his work *Prinzipienfragen der Vegetationsforschung* (1918). Later, some zoologists developed specific concepts to classify life-forms of animals, such as (a) the German entomologist Karl Friederichs (1878-1969) in his book *Die Grundfragen und Gesetzmäßigkeiten der land- und forstwirtschaftlichen Zoologie insbesondere der Entomologie* (1930, 41-45); (b) the German zoologist Adolf Remane (1898-1976) in different papers (Remane 1943; Remane 1951b); (c) the German zoologist Wolfgang Tischler (1913-2007) in his book *Grundzüge der terrestrischen Tierökologie* (Tischler 1949, 14-39); and (d) the Austrian zoologist Wilhelm Kühnelt (1905-1988) in a paper entitled *Ein Beitrag zur Kenntnis tierischer Formen* (Kühnelt 1953), reproduced in his book *Grundriss der Ökologie* (Kühnelt 1970, 106-168).

The most extensive attempt to classify animals as life-forms was carried out by the German zoologist Hans-Wilhelm Koepcke (1914-2000) in the main work *Die Lebensformen: Grundlagen zu einer universell gültigen biologischen Theorie*, published in two volumes in 1973 and 1974. Koepcke tried to build up a concept in which earthbound insights might lead to a universally oriented biology. He understood his work as a first step in discovering axioms for the ecological aspect of biological research. "Such use of axioms in biology", wrote Koepcke, "is observed only in the field of biochemistry, biophysics, physiology of the growth

[191] An ancient attempt to classify plants according to functional groups can be found in *Enquiry into Plants* (1916) by the Greek Theophrastus (c. 371-c.287 BC).

[192] According to Braun-Blanquet, Warming's system has found little acceptance, perhaps because of "its variety and lack of a coordinating principle" (Braun-Blanquet 1932, 288).

and metabolism, as well as in some branches of genetics" (Koepcke 1971, iii (my translation)). The final purpose of his efforts was the foundation of a "universal biology", making it possible to test earthbound biological insights elsewhere in the universe, for instance in investigations on the possible existence of extra-terrestrial life.[193] Adolf Remane, his former teacher, encouraged him to investigate the problem of life-forms (Koepcke 1971, viii)).

Koepcke thought that this universal biology could be reached through a method based on the term analogy. Using a great amount of data gathered from the literature[194] and his own investigations, he presented a comprehensive non-phylogenetic grouping of organisms according to functional criteria. This work is, to date, the most elaborate attempt to classify life-forms, and it is rather puzzling that it has been virtually ignored by modern biologists. His ambitious enterprise, aimed at extensively treating the phenomenon of convergence, justifies the importance of this pioneer work but it also revealed the main deficiencies of his approach. On the one hand, the broad approach supplies a rich material on convergences and stresses the value of convergence in the comparative approaches in biology. On the other hand, it could be argued that Koepcke should have restricted his analysis to fewer cases of convergences, which would have allowed him a deeper understanding of the phenomenon. However, Koepcke's broad approach is comprehensible and probably coherent with his main goal - the formulation of a "universal biology", which would allow him to make educated predictions on extra-terrestrial life. To fulfil this aim, Koepcke mainly used examples of clear adaptive features in his attempt to classify convergent adaptations through "ecological formulae" (*Oekoformel*) (Koepcke 1973, 1307-1374). This concept was implied in the work of several earlier authors and first proposed by Adolf Remane (1943). Koepcke's ecological formulae classify organisms according to the following criteria (most with several sub categories): (a) assimilation of substance (*Substanzerwerb*); (b) locomotion; (c) "resistance" (used in a very broad sense); (d) sociability; (e) brood care; and (f) sexuality. Koepcke explained that this was only a rough classification, which could be expanded and refined by the addition of further criteria. For example, he used a criterion for "grade of perfection or markedness" (*Perfektionsgrad* or *Ausprägungsgrad*) to express the differences in intensity in which living organisms carried out specific performances. Although Koepcke pointed out that he was

[193] Exobiology was the topic of one of his subsequent works (Koepcke 1975).

[194] Curiously, although an impressive number of works are referred to in the text, this book lacks a literature list; as well as an index. In a personal communication, Juliane Diller (Koepcke's daughter) wrote that a third volume of the work was planned but never published. She sent this researcher an index of the work of 133 pages which was planned for the last volume (Diller, pers. comm. on 12. September 2008).

dealing with values which are difficult to measure, his evaluations imply a high degree of accuracy which does not seem to correspond or reflect, even approximately, the complexity of the topics treated in his work. His efforts to identify degrees of adaptation are similar to early attempts to depict a certain feature found in different, not always close related species (see Figure C.1), implying a preconceived view on the evolution of these features from a more generalized to more specialized state. Although these series have a certain justification, if used to express different degrees of markedness in a certain feature, they did not consider the problems in comparing features which possibly developed under different selective pressures and therefore are not "comparable". Furthermore, these series often imply the erroneous idea that organisms develop to reach a state of perfection in the development of certain features.

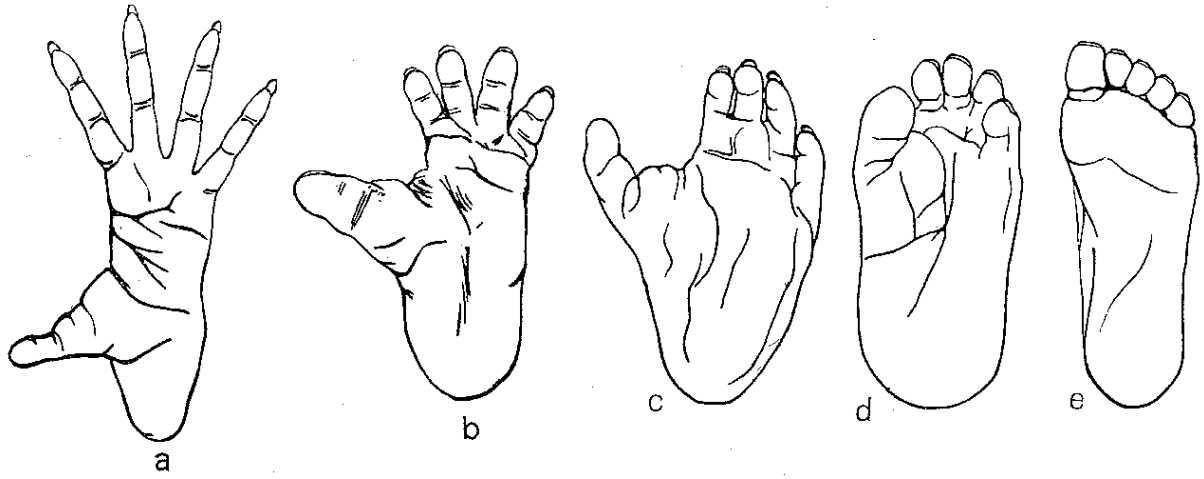

Figure C.1 Hans Böker's representation of *anatomische Reihe* (anatomical rows). He presented the feet of different organisms to illustrate the evolution of the human foot. These comparisons often reflect the author's preconceived view about how a feature developed, and therefore they supplied little insight about the complexity of organismic evolution.[195] (a) Young orangutan, (b) young gorilla, (c) adult gorilla, (d) mountain gorilla, (e) and a European; from different authors, in (Böker 1935, 151).

As the above mentioned works by Gams, Friederichs, Kühnelt, Remane, Tischler and Koepcke are less known to modern non-German speaking biologists, several independent concepts of life-forms of animals were later developed. One of the most widespread of these concepts was proposed by the American ecologist Richard B. Root, who introduced the term "guild" in animal ecology in a paper on the blue-gray gnatcatcher (Root 1967). By guild he

[195] This statement should not be interpreted as an attempt to detract Böker's merits as a biologist. Böker simply used a method which was widespread in his time. It was, for instance, extensively used by Carl Gegenbaur, see chapter C.2.2 on the concept of ascending scales in anatomical investigations. The integrative approach used in Böker's "biological anatomy" is comparable with Othenio Abel's interdisciplinary efforts. By insisting that biology, ethology, anatomy and palaeontology cannot be treated as separate fields, both authors paved the way for modern palaeobiology and ecomorphology.

understands “a group of species that exploit the same class of environmental resources in a similar way” and species “that overlap significantly in their niche requirements” (Root 1967). The American ecologist Kenneth Cummins proposed the term “functional groups” to discuss “important process-oriented ecological questions”, and the term “functional type” to describe “non-phylogenetic classification leading to a grouping of organisms that respond in a similar way to a syndrome of environmental factors” (Cummins 1974). Several plant ecology strategy schemes were proposed in the literature, arranging species in categories according to their ecological attributes, as for instance that done by Martin Westoby and contributors (Westoby 1998; Westoby et al. 2002). For a review of further functional classifications see Blaum et al. (2011), Gitay and Noble (1998), Kenoyer (1929) and Westoby (1998).

APPENDIX D – The historical roots of the savannah hypotheses

D.1 Introduction

The emergence of the early ancestors of human beings is traditionally explained in connection with an open plain-scenario, often called the "savannah theory" or "savannah hypothesis" (SH). Most versions of the savannah model suggest that proto-hominins or hominins abandoned forested or wooded habitats and gradually adapted to an open or semi-open environment. As we will see, several analogies were implied in comparisons between proto-hominins and savannah animals, mostly in attempts to corroborate long arguments leading to early hominins adapting to open plains or as incidental, but insightful remarks in palaeoanthropological publications. The discourse in which these analogies were proposed and used to connect with other palaeoanthropological evidence is then a central aspect of the present review. The results of this investigation will be integrated into a broad analysis of the use of convergence as a tool in early and modern hypotheses on human evolution (in chapter 6).

It is probably useful to quote some modern versions of the savannah scenarios to illustrate a major change occurred in the last years. The first example is a statement by Charles F. Hockett and Robert Ascher in 1964;[196] it illustrates what is here denominated "traditional SH". In this scenario, early hominin adaptation to open plains occurred simultaneously or almost simultaneously with the development of a permanent bipedalism – as an immediate response to this new environment. They wrote:

> Geological evidence suggests that at one or more times during the East African Miocene, a climatic change gradually thinned out the vegetation, converting continuous tropic forest into open savannah with scattered clumps of trees. As the trees retreated, some bands of hominoids retreated with them, never abandoning their classical arboreal existence; their descendants of today are the gibbons and siamangs. Other bands were caught in isolated groves of slowly diminishing extent. In due time, those bands whose physique make it possible for their members to traverse open county to another grove survived; those that could not do this became extinct. Thus, for those bands, the survival value of the perquisites for safe ground travel was not at all that they could therefore begin a new way of life out of the trees, but that, when necessary, they could make their way to a place where the traditional arboreal way of life could be continued. The hominoids that were successful at this included those ancestral to the great apes and to ourselves. (Hockett & Ascher 1964, 140)

[196] According to them, it is an elaboration of the brief suggestion published by Alfred S. Romer some years before (Romer 1959, 327); on Romer's SH see chapter 6.

Because of environmental changes and increased interspecific competition, early hominins were forced to abandon the forest and occupy the open plains:

> Thus, in the long run, the trees would be held by the more powerful, while the less powerful would repeatedly have to get along as best they could in the fringes of the forest or in open country. Here is a double selective process. The trees went to the more powerful, provided only that they maintained a minimum ability to traverse open country when necessary: some of these successful ones were ancestral to the great apes of today. Our own ancestors were the failures. We did not abandon the trees because we wanted to, but because we were pushed out. (Hockett & Ascher 1964, 140)

In the last years, a *lange Rochade* (German for castling long side in chess) took place in primatology and palaeoanthropology. As we will see, this event that can be partially considered as a continuation of a development which took place in the early 1960s onwards, when several authors began to compare chimpanzees living in widely different habitats. In this research, they described chimpanzees living in dry open habitat, among others, in an attempt to understand the ecological factors which were in this time believed crucial for the adaptation of early hominins to similar habitats.[197] As will be shown, it was also around this time that some authors began to stress the complexity of the palaeoenvironment of early hominins and to point out arboreal adaptations in australopithecines. This led to placing the major climatic and environmental changes and the adaptation to open plains in a later phase in hominin evolution. One example of this version – here called "late-SH" – was formulated by Ernst Mayr (1904-2005) in the final book he published. It was written in time for his 100th birthday and is a survey of controversial concepts in biology. He wrote:

> The decisive motor in human evolution was apparently a series of climatic changes. The Miocene and Pliocene were periods of increasing aridity in Africa. This drought period probably peaked around 2 million years ago. As Africa became more arid, the trees in the tree savanna suffered, more and more of them died, and the tree savanna gradually became a bush savanna. The dying of the trees deprived the australopithecines of their retreat to safety. They were completely defenseless where there were no trees. […] Some tree savannas in especially favorable places apparently retained their trees and australopithecines survived here for a while, such as *Australopithecus habilis* and the two robust species (*Paranthropus*). More importantly, some australopithecine populations evolved into *Homo* and became adapted to the bush savanna and its carnivorous inhabitants. (Mayr 2004, 199)

[197] See chapters 4 and 6, and (McGrew et al. 1981; Moore 1992) on savannah chimpanzees.

The expression "savannah hypothesis" (or "savannah theory") is rather modern. It was certainly not used regularly in palaeoanthropological literature before being used repeatedly in Elaine Morgan's publications on the aquatic hypothesis from 1972 onwards (see chapter D.6.3). However, as we shall see, the first hypotheses on the emergence of primeval man on open plains were already proposed in pre-Darwinian times. One of the main differences between these early ideas and modern SHs is related to the fact that the early models did not conceive open plains to be real geographical place, but rather as a "place of development" in opposition to the usual primate habitat as a "place of stagnation". To acknowledge these historical facts and avoid the pitfalls of using modern terms in connection with old ideas, the term "open plains hypotheses" was proposed by the author to denominate the early models (Bender 1999a, 38).[198] The term open plains hypotheses will be used here as synonym to SH, but more specifically in connection with hypotheses proposed before the evolutionary synthesis.

As a result of the strong influence of the SHs in palaeoanthropological research, it would be expected that the history of this theory has been well investigated. However, besides two unpublished works, there is, to date, only one published analysis on the origin and development of the open-plains ideas.[199] There are many possible reasons for this gap in the historical research. Firstly, previous historical analyses of the hypothetical models of early human evolution have been carried out by a relatively small group of specialists, and several basic aspects of the history of hypotheses on human evolution are still under-researched (Corbey 1995, 5). Secondly, in addition to projects conceived for other specific purposes,[200] most of the historical surveys deliver basic overviews of the topic (Bowler 1986; Delisle 2004; 2007; Eiseley 1961; Parker & Jaffe 2008), which do not allow extensive analyses of single evolutionary scenarios. Thirdly, while some excellent reviews of the latest discussion on environmental changes in palaeoanthropological hypotheses have been published recently, they have not analyzed the palaeoanthropological discussion before 1925 (Potts 1998a; Potts

[198] This term was inspired by the terminology of Hans Weinert (1887-1967), who used expressions like *Freilandtiere* (open plain animals) in connection with *Dryopithecus* and *Freilandmenschenaffen* (open plain apes) in connection with *Australopithecus africanus*; see chapter D.5.2.

[199] Several authors succinctly mentioned early ideas on primeval man abandoning forests and facing the danger of a terrestrial life or, more specifically, a life in open places (Bowler 1986, 161-170; Landau 1991, 45-47; Stoczkowski 2002, 55-77) without a detailed discussion of the SHs' early origins. The present chapter expands and develops a historical review presented in an unpublished thesis (Bender 1999a).; this work was merged with the research carried out by Nicole Bender-Oser (Bender-Oser 2004b) and published in (Bender et al. 2012); the present chapter is partially based on this publication.

[200] For instance, some works describe patterns of narrative in human evolution (Landau 1981; 1991) or identify alleged parallels between ancient and modern palaeoanthropological hypotheses (Stoczkowski 2002).

1998b; Reed 1997). One of the most important reasons for the absence of historical research on the open plains-ideas is related to the notion that the beginning of the SHs seemed to be clearly identifiable (see chapter D.4 on the discovery of *Australopithecus africanus* by Raymond Dart). As already mentioned, this opinion is not compatible with historical facts.

D.2 Aims and scope of the investigation

The following questions are in focus of the present review:

(a) How did the idea of primeval man evolving in open plains develop and how was this idea defended in anthropological discussion after 1859?

(b) Did the open plains-concept influence Dart's description of the child of Taung, or was Dart's SH inferred directly from the fossil evidence described by him in 1925?

(c) How did early anthropologists use analogies between humans and other organisms to corroborate or illustrate the existence of primeval man on open plains?

(d) How was the evidence gathered from different palaeoanthropological disciplines used to support the savannah model?

(e) Which alternative scenarios were proposed to contextualize early hominin evolution, and how does the logical corroboration of these scenarios differ from the corroboration of the SHs?

In the present chapter a representative sample of SHs published in the major European languages between 1809 and 1939 are analyzed. This timeframe is determined by two publications which established relevant aspects in the emergence and consolidation of the SHs: in 1809 Jean Baptiste de Lamarck published the first suggestion of primeval man standing upright in response to an open environment; and in 1939 Franz Weidenreich described these ideas as a "widely spread belief" (Weidenreich 1939, 87-88).

D.3 The origin of the idea of primeval man developing on open plains

As far as can be assessed, the first ideas about primeval man emerging in open plains in the framework of an evolutionary hypothesis were outlined in 1809 by the French naturalist Jean Baptiste Pierre Antoine de Monet, Chevalier de la Marck (1744-1829). In his *Philosophie zoologique* (Lamarck [1809] 2006) Lamarck describes in details how an early ancestor of primeval man abandons an arboreal life to adapt itself to open plains (English translation by Hugh Elliot):

> As a matter of fact, if some race of quadrumanous animals, especially one of the most perfect of them, were to lose, by force of circumstances or some other cause, the habit of climbing trees and grasping the branches with its feet in the same way as with its hands, in order to hold on to them; and if the individuals of this race were forced for a series of generations to use their feet only for walking, and to give up using their hands like feet; there is no doubt […] that these quadrumanous animals would at length be transformed into bimanous, and that the thumbs of their feet would cease to be separated from the other digits, when they only used their feet for walking. (Lamarck 2006, 170)

Lamarck did not specifically use the expressions "open plains" or "savannah", but, as we can see in the passage below, a "large and distant view" is not the context of a forest habitat[201]:

> Furthermore, if the individuals of which I speak were impelled by the desire to command a large and distant view, and hence endeavoured to stand upright, and continually adopted that habit from generation to generation, there is again no doubt that their feet would gradually acquire a shape suitable for supporting them in an erect attitude; that their legs would acquire calves, and that these animals would then not be able to walk on their hands and feet together, except with difficulty. (Lamarck 2006, 170)

Lamarck was not the first to propagate ideas on the role of freed hands for human beings. They were sometimes expressed by ancient authors, as for instance in the text *Memorabilia* by the Greek historian, philosopher and soldier Xenophon (ca. 431-355 BC). He wrote:

> To begin with, of all the animals, it is only human beings that they made stand upright. And upright posture makes one able to see more before one, gaze more at the things above, and suffer less that is bad. And they implanted sight, hearing, and a mouth. And then, while they gave feet to the other animals who walk, these permit them only to travel; on human beings they also included hands, which produce most of those things whereby we are happier than they. (Xenophon 1994,1, 4, § 11, translated by Bonnette)

The concept of a primeval man having freed hands to use weapons or tools also belongs to the topics discussed by philosophers of the Enlightenment in the 17th and 18th centuries, often linked to ancient theories on the origin and development of culture (see Müller 1968; Stoczkowski 2002, 124-126).

[201] This interpretation of Lamarck's ideas was also suggested in a paper *Man's posture: its evolution and disorders* by the Scottish anatomist and anthropologist Arthur Keith (1866-1955) when he stated: "From this passage we see that […] Lamarck regarded the erect posture as a result of the chimpanzee-like ancestor having abandoned an arboreal mode of life for one *in the open country*. [...] He was fully alive to the fact that any anthropoid which had acquired the human mode of progression had gained an enormous advantage; it would no longer be confined to tracts of tropical jungle but would have the *whole length and breadth of the earth open* to it" (Keith 1923, 451, italics added).

In Lamarck's view forests were not adequate enough to promote the evolution of man. Consequently, he believed that the first bipedal ancestor of primeval man would dominate and banish other primates in localities which he did not occupy, i.e. into forests or other desert places (Lamarck 2006, 170). For Lamarck it was clear that the emergence of bipedalism and freed hands and its consequences for the development of intelligence gave primeval man a decided advantage over other animals.

Lamarck's scenario of a bipedal primeval man using his free hands for purposes other than climbing trees and grasping branches – an idea previously termed "tower hypothesis"[202] by the author (Bender 1999a, 65) – was the first hypothesis on human *bipedalism*[203] embedded within an evolutionary context. Similar models were regularly presented in several publications from the late 19th century onwards (see, e.g., Baer & Hellwald 1874, 526-528; Keith 1923; Knauer 1916; Koch 1929, 54; Munro 1897, 90-93; Osborn 1919, 60; Reinhardt 1906, 6; Suschkin 1933). For instance, Franz Koch (1929, 54), in an early attempt to corroborate his views on the emergence and dissemination of early man with help from Alfred Wegener's theory of continental drift, wrote about the emergence of an erect posture for purposes of vigilance and defence: "The primeval man, his wife and children probably had to stand up to an incessant search for enemies and prey and frequently betake themselves to flight" (Koch 1929, 54, my translation). Koch gave no specific source of these views, which suggests that this idea had been defended already by other authors. Different versions of the tower hypotheses (today often called "vigilance hypothesis") were defended in the three decades subsequent to the evolutionary synthesis of the 1930s and 1940s (Emiliani 1968; Heberer 1973, 34; Ravey 1978; Robinson 1963, 401; Robinson 1972, 257; Washburn & DeVore 1961) and are still stated in palaeoanthropological and primatological literature.

Sixty-two years after Koch's publication, Charles Darwin had published the *Descent of Man* with his own ideas on the evolution of man. In this book he expressed what it seems to be a strongly summarized version of Lamarck's scenario of a primeval man leaving the forest and adapting to open plains:

> As soon as some ancient member in the great series of the Primates came, owing to a change in its manner of procuring subsistence, or to a change in the conditions of its native country, to

[202] Modern versions of this idea are usually called "vigilance hypothesis". Although modern models rescinded statements suggesting "a trend to evolve" in early hominin evolution, they show a remarkable similarity with Lamarck's tower hypothesis, often mentioning the aspect of vigilance against predators.
[203] Although Benoît de Maillet should be considered the first naturalist to devote a book on evolutionary ideas, he did not consider human bipedalism in his book *Telliamed*; see Appendix B.

> live somewhat less on trees and more on the ground, its manner of progression would have been modified; and in this case it would have had to become either more strictly quadrupedal or bipedal. (Darwin 1871, vol. 1, 140-141)

The similarity between the ideas of Lamarck and Darwin relies not only on the same overall adaptive scenario exposed by both authors (an arboreal primate abandoning the forest, occupying an open landscape and developing habitual bipedalism in response to the new environment), but also on the identification of two alternative reasons for the evolutionary phenomenon: Lamarck's picture of a primate abandoning the forests "by force of circumstances or some other cause" (Lamarck 2006, 170) correlates with Darwin's scenario (quoted above) of a primate adapting to a more terrestrial life "owing to a change in its manner of procuring subsistence, or to a change in the conditions of its native country" (Darwin 1871, vol. 1, 140). It is therefore not surprising that at least one early historian pointed to the strong coincidences in the open plains scenarios of both authors. When commenting on Lamarck's open plains ideas, the American entomologist and palaeontologist Alpheus Packard succinctly stated:

> This is certainly, for the time it was written, an original, comprehensive, and bold attempt at explaining […] the probable origin of man from some arboreal creature allied to the apes. It is as regards the actual evolutional steps supposed to have been taken by the simian ancestors of man, a more detailed and comprehensive hypothesis than that offered by Darwin in his *Descent of Man*, which Lamarck has anticipated. (Packard 1901, 371)[204]

Some years later, Ludwig Wilser was surprised about the modernity of Lamarck's open plains ideas. After quoting Lamarck, he pointed out that there is nothing really wrong with his account of human evolution, even taking into consideration "the advanced knowledge and science of our day" (Wilser 1910, 59-60, my translation). Mayr also pointed out that Lamarck's hypothesis "is startlingly modern" (1982, 352), and Delisle came to a similar conclusion when he stated: "Lamarck's view is modern in that it is fairly close to what we believe today to be true" (2007, 43). Similar statements emphasising the modernity of *Darwin's* open plains ideas were also expressed by palaeoanthropologists. For instance, when discussing Darwin's views on the evolution of man, Nesturch described a modern SH:

[204] The negative connotation of Packard's statement should be qualified, as he wrote these words from the perspective of a proponent of Neo-Lamarckism. Nevertheless, in one point Packard is right: Lamarck's hypothesis on the evolution of primeval man was the most elaborate until 1863, when Thomas Huxley, Carl Vogt and Charles Lyell published their works on the subject (Huxley 1864 [1st ed. 1863]; Lyell 1863; Vogt 1863).

> As a result of changes in the natural conditions, mainly due an opening of the forests in their home, our ancestors were forced to abandon the trees in their search for food and live on the ground in a wooded steppe [*Waldsteppenlandschaft*]. Later they occupied completely open landscapes. (Nesturch 1961, 25, my translation)

In this quotation, Nesturch did not specify which were Darwin's original ideas and which were the SHs developed after 1871; in doing so, he implied a strong similarity between Darwin's open plains ideas and the SHs defended in the 1960s. Finally, to give some recent examples: McHenry wrote that "Darwin's view of the origin of bipedalism remains useful" (1982, 156); and Tobias observed that "There had been a long-standing hypothesis, going back to Charles Darwin and then to Raymond Dart and Robert Broom, that early human evolution occurred in a savanna environment. I grew up with this paradigm and it had acquired an aura of sanctity" (2004, 388).

However, these indications cannot be interpreted as definitive evidence that Darwin's SH was directly inspired by Lamarck's open plains scenario. Darwin, of course, well knew of Lamarck's *Philosophie zoologique* (Darwin 1897, xix),[205] but he did not quote Lamarck (or any other author) in relation to his own SH. In later editions he included a "Historical Sketch" in which he recognised Lamarck (among many others) as pioneering the evolutionary idea (Darwin 1897, xiv), yet at the same time he pointed out Lamarck's erroneous views on "a law of progressive development" (Darwin 1897, xv), which Darwin justifiably could not endorse. In private correspondence Darwin did not appreciate references to his own evolutionary ideas as a modification of Lamarck's doctrine of development and progression (see Gould 2002, 193-197). This is especially evident in a letter to Charles Lyell dated 12-13 March 1863:

> Lastly, you refer repeatedly to my views as a modification of Lamarcks doctrine of development & progression; if this is your deliberate opinion there is nothing to be said −; but it does not seem so to me; Plato, Buffon, my grandfather before Lamarck & others propounded the *obvious* view that if species were not created separately, they must have descended from other species: & I can see nothing else in common between the Origin & Lamarck. I believe this way of putting the case is very injurious to its acceptance; as it implies necessary progression & closely connects Wallace's & my views with what I consider, after two deliberate readings, as a wretched book; & one from which (I well remember my surprise) I gained nothing. (Darwin 1999, 222-223)

[205] Darwin had a copy of the 1830 printing of *Philosophie zoologique* (see Hull 1985, 802). For Darwin's references to Lamarck's evolutionary ideas see Schilling (1990) and (Egerton 1976).

From these words it is understandable that Darwin avoided quotations of Lamarck's views as supporting his own ideas, limiting himself to the formal acknowledgment of Lamarck as one among many precursors of the evolutionary idea. The present study does not intend to contribute here to the discussion on Lamarck's possible influence on Darwin's evolutionary views. Basically, I agree with Ernst Mayr when he suspected that "Darwin vastly underestimated the role which Lamarck had played in preparing the intellectual climate for the subsequent Darwinian advances" (Mayr 1972, 90). This view is also defended by some other historians of science (Corsi 1978; Gould 2002, 194). On the other hand, Darwin's alleged failure to properly acknowledge previous naturalists is sometimes based on a complex set of factors, which cannot simply be explained as Darwin's intellectual antipathy towards these authors or concerns about overemphasis of the pioneering work of others. A revealing and widely ignored example for this complexity is related to one of Darwin's ideas, which I once named "*Darwins Inseltheorie*"(Darwin's island hypothesis) (Bender 1999b, 111). This topic will be dealt with in the next section.

D.3.1 Darwin's island hypothesis and possible reasons for his failure to acknowledge certain authors

Darwin speculated in *Descent* on the possibility that a "helpless" primeval man could have developed first on a large island, where he would not be confronted with dangerous predators:

> But granting that the progenitors of man were far more helpless and defenceless than any existing savages, if they had inhabited some warm continent or large island, such as Australia or New Guinea, or Borneo (the latter island being now tenanted by the orang), they would not have been exposed to any special danger. In an area as large as one of these islands, the competition between tribe and tribe would have been sufficient, under favourable conditions, to have raised man, through the survival of the fittest, combined with the inherited effects of habit, to his present high position in the organic scale. (Darwin 1871, vol. 1, 157)

Darwin did not mention that John Frederick William Herschel (1792-1871) had already suggested a connection between human as helpless creatures and the refuge in islands in tropic regions like humans survive?" In the first page of his work *A Preliminary Discourse on the Study of Natural Philosophy*, first published in 1830, Herschel wrote:

> The situation of man on the globe he inhabits, and over which he has obtained the control, is in many respects exceedingly remarkable. Compared with its other denizens, he seems, if we regard only his physical constitution, in almost every respect their inferior, and equally unprovided for the supply of his natural wants and his defence against the innumerable

> enemies which surround him. No other animal passes so large a portion of its existence in a state of absolute helplessness, or falls in old age into such protected and lamentable imbecility. (Herschel 1831,1)

In the same paragraph Herschel envisaged a non-evolutionary scenario in which man could have some chances to linger:

> Remarkable only for the absence of those powers and qualities which obtain for other animals a degree of security and respect, he would be disregarded by some, and hunted down by others, till, after a few generations, his species would become altogether extinct, or, at best, would be restricted to a few islands in tropical regions, where the warmth of the climate, the paucity of enemies, and the abundance of food, might permit it to linger. (Herschel 1831, 2)

It is highly problematic to interpret the obvious similarity between the ideas of Herschel and Darwin as mere coincidence. It is well documented that Herschel's work was influential in Darwin's career (Gildenhuys 2004; Ruse 199313-33; Warner 2009), so this subject will not be treated in detail here. Darwin not only knew and acknowledged Herschel's book *A Preliminary Discourse*, but also considered it as fundamental to his work as a naturalist, as he freely admitted in his autobiography:

> During my last year at Cambridge, I read with care and profound interest Humboldt's *Personal Narrative*. This work, and Sir J. Herschel's *Introduction to the Study of Natural Philosophy*[206] stirred up in me a burning zeal to add even the most humble contribution to the noble structure of Natural Science. No one or a dozen other books influenced me nearly so much as these two. (Darwin 1958, 67-68)

What is probably more relevant than the simple similarity between the statements of Darwin and Herschel is that Darwin's island hypothesis is diametrically opposed to other statements expressed in his Descent, where he speculated on the birthplace and antiquity of man:

> We are naturally led to enquire where was the birthplace of man at that stage of descent when our progenitors diverged from the Catarhine stock. The fact that they belonged to this stock clearly shews that they inhabited the Old World; *but not Australia nor any oceanic island, as we may infer from the laws of geographical distribution*. In each great region of the world the living mammals are closely related to the extinct species of the same region. It is therefore probable that Africa was formerly inhabited by extinct apes closely allied to the gorilla and

[206] Darwin meant *A Preliminary Discourse on the Study of Natural Philosophy*. The deviation in the title is due to the fact that Herschel's book was initially the introductory volume to *Cabinet Cyclopedia, edited by* Dionysius Lardner.

> chimpanzee; and as these two species are now man's nearest allies, it is somewhat more probable that our early progenitors lived on the African continent than elsewhere. (Darwin 1871, vol. 1, 199, italics added)

This almost[207] unnoticed amazing contradiction indicates that Darwin's island hypothesis was not developed in consonance with the bulk of arguments presented in other parts of his work. One can assume that it is difficult to classify as mere coincidence the similarities between Lamarck's and Darwin's open plains views (as well as the similarities between Herschel's and Darwin's island hypotheses). However, this is not to accuse Darwin of plagiarism or to doubt on his integrity. Contrary to the passionate conclusions expressed by early anti-Darwinists (see, e.g., Kohlbrugge 1915), the opinion of most historians is shared here: that Darwin's work is a landmark in evolutionary biology. He was undoubtedly an original genius, but he was nevertheless anticipated by some earlier authors concerning the formulation of some specific ideas. Darwin was working with a prodigious amount of data obtained both from publications or directly supplied through personal communications in the correspondence with other naturalists. After years of intensive research it seems that it was increasingly difficult for him to draw a sharp line between original ideas and information he obtained from the literature. It may be that Darwin reformulated Herschel's statements in an evolutionary context, inserted it in the chapter on the cradle of mankind, and subsequently forgot to check the compatibility of these ideas with his own concepts expressed in other chapters in the same book. However, why should Darwin not mention Herschel's authorship in connection with the island hypothesis? When I addressed this question to Darwin's expert Mario Di Gregorio[208], he pointed out that Darwin made great efforts to present his evolutionary ideas as a contribution to natural science and not to a philosophical debate. This is a plausible explanation for the absence of any acknowledgement of Herschel, since Herschel's island hypothesis was proposed in a work on natural philosophy.

To sum up, the hypothesis that Darwin's open plains ideas were inspired by Lamarck seems corroborated by the different facts. It would be however misleading to consider Darwin's

[207] It is remarkable that this evident incongruence is ignored by historians of science, but was identified by an early author interested in finding misconceptions in Darwin's work. In his book *Homo Versus Darwin: A Judicial Examination of Statements Recently Published by Mr. Darwin Regarding "The Descent of Man"*, William Penman Lyon (1812-1877) presented his thoughts in the form of a judicial enquiry. He wrote: "How can Mr. Darwin make such a supposition [on helpless primeval man surviving on a large island like Australia or New Guinea, or Borneo], my Lord, when he says elsewhere, "the fact that they (man's progenitors) belonged to this (the Catarhine) stock, clearly shows that they inhabited the Old World ; but not Australia, nor any oceanic island, as we may infer from the laws of geographical distribution?" (Lyon 1872, 81).

[208] In his talk *Charles Darwin: His methods of work and their influence on how he conceived and shaped his theories* (1st of March 2011, Faculty of Health Sciences, University of Cape Town).

failure to acknowledge Lamarck's open plains ideas as plagiarism. It is possible that Darwin was inspired by Lamarck's open plains ideas but simply forgot where he first read about it. It is not impossible that Darwin avoided acknowledging Lamarck in connection with an idea that Darwin perceived as so obvious that a reference to a similar idea expressed by an earlier author would be redundant. Finally – and closely related to the latter explanation – it cannot be completely excluded that Darwin did not pay attention to Lamarck's open plains ideas and convergently developed the same idea; this topic is treated in the next section.

D.3.2 The intuitive passage from an arboreal to a terrestrial mode of life

The picture of an arboreal ancestor of man abandoning the trees and adapting to open plains is an intuitive one. It is strongly connected to the ancient dichotomy of non-human primates living on forest / humans living outside of forests. This dichotomy is reinforced by the idea of forest as a place which accommodates "progressive" non-human animals or – at the other end of the comparison between humans and other animals - what was once believed to be primitive human races "still living" on forests. These ideas can be identified for instance in the myths of wild men (Bernheimer 1970; Husband 1980), in the Eurocentric comparisons between non-human primates and allegedly "primitive humans" (Corbey 2005; Duchet 1995; Gerbi 2010; Hodgen 1971; Thijssen 1995; Thomas 1983) and in the innumerable anthropomorphic depictions of non-human primates, for instance holding a stick in the hand.[209]

The idea of humans living first in woodlands and then, with the passage of time, becoming inhabitants of open land already had been expressed outside the context of evolutionary thinking. One early example concerns the statements by William Pownall (1722-1805), Governor of Massachusetts from 1757 to 1760, in a book *An Antiquarian Romance Endeavouring to Mark a Line by which the Most Ancient People and the Processions of the Earliest Inhabitancy of Europe may be Investigated*, first published in 1795. In this account of the history of the European races based on ancient authors, Pownall described first humans as "woodland-men" or "Sylvan men", who did not have the same opportunities to become as prolific as "land-workers". He wrote:

> Whilst men continued living the *Sylvan life*, gathering the spontaneous vegetables and fruits of the woods, or as hunters catching the wild animals of the forest, for their food; they would,

[209] Primates staying or walking with sticks – see figures in (Bender 1999a; Spencer 1995) – were not only depicted in zoological treatises, but also sometimes described in travel books, as for instance by the Muslim traveller Ibn Baṭūṭah (1304-ca. 1368) (Ibn-Battuta 1858, vol. IV, 176).

> from the mode of that life, and from the nature of that occupation, multiply but slowly. […] The Sylvan Hunter Nation, from principle, never could be prolific and populous, and in fact never was. (Pownall 1795, 136-137)

The idea of humans descending from "less progressive" animal forms (= e.g., creatures walking on four legs and the body entirely covered with fur) was even expressed within theological discussions. One interesting example can be found in a widely ignored booklet entitled *Taschenbuch der Vorzeit* (Pocketbook of Antiquity) published in 1805 by the German mathematician, historian and architect Jacob Friedrich von Rösch (1743-1841). The booklet was conceived as an extract of a future publication.[210] Within a discussion on Preadamism Rösch, wrote the following, quite remarkable passage on Adam as a kind of wild man (= human with animalistic features):

> Adam probably lost sight of humans in his childhood, grew up among animals of the field, has been running on all fours, and did not know from whom he received his existence. During a great inundation or deluge which took place in his time, his skill in running and climbing helped him to escape the rising water[211]. (Rösch 1805, 4-5, my translation)

The idea of progressive humans evolving "outside of forests" was the most logical consequence of early attempts to envisage human evolution. Although the terms "open plains", "savannah" or "open glades" in connection with human evolution was only sporadically used in the 19th century (Wallace 1889, 459) and early 20th century (Keith 1923; Weinert 1932, 209; Wells et al. 1931, 536), the primary early human adaptation to open plains or forest margins was usually regarded as a fact. This idea was not only implied, but was also sporadically explicitly stated, as for instance by the British naturalist and evolutionist Alfred Russel Wallace. In following statement he touched not only the dichotomy "forest / open plains", but used this idea to created a more specific dichotomy, which is based on the polarization "tropic environment = forests = place of stagnation" / "subtropical zone = open

[210] This was published in 1819 under the title *Beiträge zur Geographie und Geschichte der Vorzeit*. Rösch discussed also Ballensted's work *Die Urwelt oder Beweis von dem Daseyn und Untergang von mehr als einer Vorwelt* (Rösch 1819, 441-456). As mentioned in Appendix B, chapter B.3, Ballensted wrote about gradual evolutionary changes in living organisms and knew and *Telliamed* from the secondary literature. Rösch's and Ballensted's works are impressive examples of theological discourse leading to ideas evoking evolutionary phenomena as soon as speculations were not restricted by the time frame and narrative imposed by the Bible. In fact, as soon as Adam was not considered the first human, completely new perspectives were open regarding what was "before Adam".

[211] Adam hat sich wahrscheinlich in seiner Kindheit von den Menschen verloffen [*„verlaufen"* in modern German], ist unter den Thieren des Feldes aufgewachsen, auf allen vieren geloffen [gelaufen], und wusste nicht von wem er sein Daseyn erhalten. Bei einer zu seiner Zeit erfolgten grossen Ueberschwemmung oder Sündfluth half ihm seine erlangte Fertigkeit im Laufen, Steigen und Klettern dem Anlaufe des Wassers zu entrinnen.

plains (or high plateaus) = place of development". He used this dichotomy to reinforce his ideas on humans developing in a more "vigorous" environment outside of the tropics[212]:

> It has usually been considered that the ancestral form of man originated in the tropics, where vegetation is most abundant and the climate most equable. But there are some important objections to this view. The anthropoid apes, as well as most of the monkey tribe, are essentially arboreal in their structure, whereas the great distinctive character of man is his special adaptation to terrestrial locomotion. We can hardly suppose, therefore, that he originated in a forest region, where fruits to be obtained by climbing are the chief vegetable food. It is more probable that he began his existence on the open plains or high plateaux of the temperate or sub-tropical zone [.] (Wallace 1889, 459)

This popular use of a specific principle of parsimony in the interpretation of early human evolution – the only conceivable environment to contextualize primeval man's evolution was "on the ground" and "outside of the forest" – supplied the rationale to formulate several concurring hypotheses addressing the exact way in which early hominins interacted with this new environment. When focusing on the multiple ideas proposed within the SHs' framework, early scientists did not challenge the general scenario of a primeval man adapting to the open plains; they rather accepted the assumption to be a fact. The early roots of the open plains ideas became eclipsed when fossil evidence discovered by Raymond Dart became an integral part of this discussion; this topic will be discussed in the next section.

D.4 The role of fossil evidence: Raymond Dart as alleged pioneer of the savannah hypotheses

D.4.1 The discovery of *Australopithecus africanus* and the formulation of the savannah hypothesis

The Australian palaeoanthropologist Raymond Dart (1893-1988) is sporadically mentioned in connection with the SHs, or presented as the first proponent or among the pioneers of these ideas (Boesch-Achermann & Boesch 1994; Cerling et al. 2011; Potts 1998b; Reed 1997; Roede et al. 1991; Susman 1987; Verhaegen 1991). Implied in these views is the idea that the SHs arose through the discovery of crucial empirical data – in this case through the ground-

[212] This idea sometimes implies the Eurocentric concept of humans in the tropics as inferior to groups living in subtropical zones. Wallace's statement is remarkably similar to the ideas expressed by Moriz Wagner in 1870 and posthumously reprinted in 1889 (see below, chapter D.5.1). As we will see, views on primeval man's evolution influenced by a harsh environment (e.g., cold or arid climate, presence of predators) are among the most characteristic aspects of early open plains ideas. The idea of a humans of tropical countries as inferior to humans living in colder regions was criticized by the Brazilian doctor Antônio da Silva Melo in his book *A superioridade do homem tropical* (Melo 1965).

breaking discovery of the fossil named "Taung child" (*Australopithecus africanus*) described by Dart in 1925. Dart's status as pioneer of the SHs is not a mere footnote concerning academic authorship. It reveals a fundamental aspect on the role of fossil evidence in the formulation or falsification of hypotheses in palaeoanthropology and has therefore to be investigated in detail. For good reason, historians of science usually disparage "precursor-hunting", – or attempts to identify precursors for current ideas without paying enough attention to their specific historical context. However, little attention was given to the readiness in accepting the interpretation of fossil evidence as the beginning of a new hypothesis, although this model was widespread in palaeoanthropological discussion at the time. Since the historical events of the discovery, description and reception of *Australopithecus africanus* belong to the best-described topics in the history of palaeoanthropology (Dart & Craig 1959; Delisle 2007, 222-265; Gundling 2005; Kuykendall & Štrkalj 2007; Tobias 1984a; Tobias 1998; Wheelhouse & Smithford 2001), the present chapter analyses only some specific aspects of Dart's palaeoanthropological work and his alleged status as pioneer of the SHs.

Dart was born in Australia, where he received his medical training. After working under the anatomist Grafton Elliot Smith (1871-1937) at the University College London, he arrived in South Africa in 1923 to assume the position of Professor of Anatomy at the University of the Witwatersrand Medical School. In 1924 Dart received two crates of fossil-bearing rocks ("breccia") recovered at a site known as Taung (then mistakenly considered to lie in Bechuanaland), in South Africa. One crate contained the facial skeleton and the fossilized endocranial cast of a juvenile primate specimen, which came to be known as the "Taung child". Soon after he removed the matrix from the face of the Taung child,[213] Dart prepared a report for the journal *Nature*. This appeared on February 7, 1925, with the title "*Australopithecus africanus*: the man-ape of South Africa" (Dart 1925). Dart named this fossil form *Australopithecus africanus* (the "southern ape of Africa"), regarding it as basically an ape with some human-like features.

In his classic paper on the Taung child published in 1925, Dart expressed the first hypotheses on the evolutionary significance of several features of *A. africanus* and outlined a scenario to contextualize the emergence of this species (Dart 1925). He believed that through bipedalism the hands of the first hominins were freed from their more primitive function of accessory

[213] Though Dart separated the upper and lower jaws only four years later, on July 10, 1929; see (Dart & Craig 1959, 59).

organs of locomotion. The hands, he observed, were assuming a "higher evolutionary rôle" as instruments of the growing intelligence and as organs of offence and defence, allowing the absence of "massive canines and hideous features" in our ancestors (Dart 1925, 197).

Dart was evidently inspired by Darwin in connection with the formulation of his arguments on the role of the open plains in hominin evolution. As shown above, Darwin's views on the role of an open environment in the emergence of primeval man were expressed in succinct passages in which he speculated about the theoretical advantage of human bipedalism (Darwin 1871, vol. 1, 140-141). In the same chapter of *Descent* Darwin wrote: "No country in the world abounds in a greater degree with dangerous beasts than Southern Africa"(Darwin 1871, vol. 1, 157). Dart quoted this passage to underline his own ideas about the role of open plains as a harsh environment in hominin evolution in his *Nature* paper of 1925:

> […] in my opinion, Southern Africa, by providing a vast open country with occasional wooded belts and a relative scarcity of water, together with a fierce and bitter mammalian competition, furnished a laboratory such as was essential to this penultimate phase of human evolution. (Dart 1925, 199)

Dart believed that the enhanced cerebral power of early hominins made their existence possible in an "untoward environment", described as "more vast open veldt country where competition was keener between swiftness and stealth, and where adroitness of thinking and movement played a preponderating role in the preservation of this species " (Dart 1925, 199). He emphasised the desert or semi-desert ecology of the Taung area as supporting his interpretation of the status of the Taung child:

> It will appear to many a remarkable fact that an ultra-simian and pre-human stock should be discovered, in the first place, at this extreme southern point in Africa, and, secondly, in Bechuanaland, for one does not associate with the present climatic conditions obtaining on the eastern fringe of the Kalahari desert an environment favourable to higher primate life. (Dart 1925, 198)

The idea of a harsh environment as influential in the origin of primeval man became one of the most important factors in the SHs. However, Dart did not play any crucial role in the early development of this idea: on the one hand, as already mentioned in connection to Wallace's ideas and as it will be shown below, the connection "harsh-environment / human evolution" was already defended by influential authors before 1925; on the other hand, as we will see, this idea became popular in a time in which Dart's views on the hominin status of

Australopithecus africanus were rejected by most specialists in the years following the first description of the child Taung. I suspect that the most important aspect of Dart's stressing a semi-arid environment for *A. africanus* might not primary has been an attempt to stress the harsh conditions of the place. Aware that other specialists would not agree with his views of the hominin status of the Taung of child (see below, chapter D.4.2), Dart was probably trying to prevent the attack of these specialists by presenting the species as evolving in an environment considered as completely untypical for an ape but feasible for an ancestor of humans; this is the topic of the next section.

D.4.2 The hominin status of *Australopithecus africanus*: Keith's analogy with an Artic species and issues concerning big brains

Most scientists at this time did not accept the Taung discovery as relevant for the reconstruction of hominin phylogeny. In spite of Charles Darwin's prediction that Africa would prove to be the cradle of humankind (Darwin 1922, 240), most scholars opined that the emergence of the first hominins occurred in Asia. The scarce fossil evidence at this time included several Neandertal remains, the Cro-Magnon man discovered in 1868 in southwest France, the fraudulent "Piltdown Man" with a deliberately contrived combination of ape-like and human-like features (see below), the remains of *Pithecanthropus erectus* (first named *Anthropopithecus*, now *Homo erectus*) found in the 1890s in Eastern Java and "Boskop Man" found at Boskop in the South African Transvaal.[214] Dart was not unaware of the possible controversy of his Taung find in Africa: "Up to the year 1924", he later wrote in his autobiography, "South Africa was virtually unknown anthropological territory" (Dart & Craig 1959, 20).

One of the arguments against the hominin status of *A. africanus* was based on the morphological similarities that juvenile apes and modern humans share (Keith et al. 1925; Keith 1931, 115f). It was difficult to refute this argument, since one popular idea proposed during this time by the Dutch anatomist Louis Bolk (1866-1930) suggested that modern humans are sexually mature ape foetuses (Bolk 1926), a hypothesis further developed by some other scholars.[215] A typical comment on the discovery of *A. africanus* was expressed by

[214] This fossil was described in *Nature* by Dart (1923) and had been named *Homo capensis* by Broom (1918); for many years it was regarded as *Homo sapiens*.

[215] See, e.g., Schindewolf (1936, 46pp., 56pp.) and Eiseley (1947). Dobzhansky, (1962, 196), pointed out the hypotheses defending man's similarity to simian foetus: "That this pattern suggests a fetalization is an interesting fact, but by itself it throws little light on the natural selective processes that must have operated in human evolution." This statement probably still reflects the opinion of most palaeoanthropologists. For a critical discussion, see e.g., McKinney and McNamara, (1991, 291); Menke, (2007).

the Swiss zoologist and palaeontologist Adolf Naef (1883-1949). The title of his article - *Der neue Menschenaffe* (*The new ape*) (Naef 1925) - makes clear his opinion that he did not accept the hominin status of this fossil species. For him the Taung child was just a new ape species, and although he thought that the brain of Taung child was remarkably big for an ape, he saw this as evidence that among early primates some were more intelligent than today's apes. Moreover, as we will see below, he used this fossil to corroborate his idea that the early ancestors of man were less specialised than today's apes and that hominin phylogeny is much older than was commonly assumed.

The age of this fossil was also an important aspect of this debate. Dart wrote in his autobiography: "The final answer about the age of *Australopithecus* still eludes us" (Dart & Craig 1959, 50). He claimed a Pliocene age for the Taung skull (Dart 1929), but many authorities were of course dissatisfied that he was not able to supply geological evidence of age, regarding it as early Pleistocene – which was too late for most scientists to consider it as relevant to the discussion of the early evolution of our own species. In fact, some early evolutionists had already expressed the notion that a large time span should be calculated to allow for hominins to develop gradually from an arboreal ancestor. Some authors, such as Samuel Laing (1812-1897), were convinced that primeval man originated so long ago that researchers were rather pessimistic about the possibility of finding any fossil evidence. Laing wrote that the evolution of man is "to be sought as far back as the Miocene", therefore, "we can hardly expect to find many specimens of the missing link" (Laing 1889, 97). And although Thomas Henry Huxley (1825-1895) was less pessimistic than Laing, he also saw primeval man as a creature living rather far back in the past:

> Where, then, must we look for primeval Man? Was the oldest *Homo sapiens* pliocene or miocene, or yet more ancient? In still older strata do the fossilized bones of an Ape more anthropoid, or a Man more pithecoid, than any yet known, await the researches of some unborn paleontologist? Time will show. But, in the meanwhile, if any form of the doctrine of progressive development is correct, we must extend by long epochs the most liberal estimate that has yet been made of the antiquity of Man. (1864, 159)

The Scottish anatomist Sir Arthur Keith (1866-1955) was an influential opponent of Dart's views concerning the hominin status of *A. africanus.* Keith's criticism was addressed not only to the anatomy of *A. africanus*, but also focused on what he thought would be the most probable environment of Taung. In 1931 he wrote:

> If we suppose that the forest belt of tropical Africa, now inhabited by the gorilla and chimpanzee, had extended a thousand miles farther towards Cape Colony than it now does and that the great Kalahari desert was at one time green with vegetation and covered with forest, then there would be no difficulty in explaining how anthropoid apes, practising the gait of the gorilla or of the chimpanzee, came to occupy the district which is now British Bechuanaland. (Keith 1931, 114)

Keith's logic was based on the following tautological argumentation: if apes live in forests, and if *A. africanus* is an ape, then "[…] it would be legitimate to cite the discovery of the Taungs skull as evidence that South Africa had at one time been covered with jungle" (Keith 1931, 114). He illustrated his views with an analogy: "We accept the fossil remains of Arctic species as evidence of a former severity of climate. On the same grounds we should accept the fossil remains of an anthropoid ape as evidence of a vegetation in South Africa which suits anthropoid needs" (Keith 1931, 114). Dart's key supporter Robert Broom refuted Keith's assertion that Australopithecus lived in a forest environment. In his monograph *The South African Fossil Ape-Men: The Australopithecinae* (Broom & Schepers 1946) - probably the most influential earlier work supporting Dart's views on the systematics of *A. africanus* -, he wrote:

> When Keith argued in favour of the Kalahari having once been a forest land we knew practically nothing of the fossil animals associated with the Taungs ape. These fossils prove I think quite conclusively that when Australopithecus lived Bechuanaland was practically desert. (Broom & Schepers 1946, 30)

The debate between Dart, Broom and Keith on the ecology of the Taung area shows how anthropologists' views on systematics – in this case, the different opinions about the hominin status of *A. africanus* – can strongly influence their views on the palaeoenvironment of a certain species. It would be conceivable for Dart to assume that climatic changes restricted and thinned forest areas and caused the appearance and extension of open plains in Taung, and that *A. africanus* emerged when it was forced to adapt itself to the new conditions of life. In fact, hypotheses stressing the relationship between climatic changes and the evolution of organisms were already popular at this time. For instance, several authors used climatic changes as a crucial factor to contextualize the evolution of horses (see, e.g., Matthew 1913)

and humans.[216] Such climatic determinism would be compatible with Keith's idea that the Taung area was once forested.

However, as already stated above, even before his first publication on the Taung child, Dart was aware that every attempt to present *A. africanus* as ancestral to humans or closely related to our ancestors would meet with criticism.[217] With his "Taung was already semi-arid" scenario, he had at least two advantages. For one, he was able to present early hominin evolution in connection with a "harsh environment", one of the most characteristic elements of early open plains hypotheses at this time. Secondly, he was able to corroborate his ideas with geologic research on climate fluctuations carried out by Arthur William Rogers (1872-1946), at that time director of the South African Geological Survey.[218]

In a letter published in *Nature* in 1947, Keith finally recognised that Dart was right concerning the hominin status of *A. africanus*: "[…] I am now convinced on the evidence submitted by Dr. Robert Broom that Professor Dart was right and I was wrong" (Keith 1947, 377). It is ironic to note that modern palaeoenvironmental research[219] shows that Keith was probably right in his assumption about the palaeoecology of South African sites, although his opinion was based on an erroneous interpretation of the systematics of *A. africanus*.

More important than the early criticism connected to the initial palaeoenvironmental discussion was the anatomical evidence. In fact, many scientists had problems accepting a species with such a small brain as the Taung child possessed as an ancestor of modern humans.[220] The popular expectation at this time was that the emergence of bipedalism was related to an early development of a big brain. This idea was supported by the "Piltdown Man", a supposed fossil human ancestor found between 1911 (or 1908) and 1915 in a gravel pit at Piltdown, Sussex, England (see references below). The Piltdown fossil showed a peculiar combination of modern human and ape-like features – part of a modern-human-

[216] (Arldt 1907a, 606; 1907b; Eickstedt 1925; Hilzheimer 1921; Matthew 1950 [1st ed. 1915], 7, 41-44; Reinhardt 1906, 6-9; Steinmann 1908, 266).
[217] Dart [in (Dart & Craig 1959, pp. 15-16)], wrote: "I prepared a report based on my conclusions for *Nature*, the British scientific journal, half anticipating the skepticism with which it would be greeted [.]"
[218] (Dart 1925, 198), wrote: "It is generally believed by geologists (Rogers 1922) that the climate has fluctuated within exceedingly narrow limits in this country since Cretaceous times." Dart still defended this view in his autobiography published 34 years later (Dart & Craig 1959, 7).
[219] See, e.g., Bamford (1999). Her research implies that rainfall was higher during the Pliocene, suggesting that gallery forests in Sterkfontein were widespread at that time instead of the grassland of today. She even found fossil woods that have been identified as liana in *Australopithecus* deposits, dated 2.6-2.8 Ma. See also Cadman and Rayner (1989).
[220] See however above on Naef. Although he did not accept *A. africanus* as a primeval man, he seemed to regard its brain as larger than that of a modern ape.

looking calvaria and the broken right half of a very apelike mandible. This primitive jaw seemed to reveal the sequence of evolutionary change in human phylogeny: that the large brain seemed to have been already developed in early ancestors of modern humans. From the end of the 1930s scientists' attitudes about the hominin status of australopithecines began to change gradually. The "juvenile-argument" was invalidated by Dart's closest ally Robert Broom (1866-1951), one of the first scientists who accepted the hominin status of the Taung child. After 1936 Broom discovered many adult specimens of *A. africanus*, showing that the hominin features are also present in the adult forms. In 1941 he summarized his views in a *Nature* paper: "The South African caves have shown us that there lived in Pleistocene times various anthropoids which in many characters were much nearer to man than to the living anthropoids. They had larger brains, and almost the human type of teeth, and there is considerable reason to believe they were mainly bipedal" (Broom 1941, 13). Most of this interpretation is still valid today. From 1953 to 1955 Joseph Weiner, Kenneth Oakley and W. E. Le Gros Clark exposed the Piltdown fossil as a hoax.[221] After this exposure the "small brain" and other anatomical characteristics of *A. africanus* were definitively accepted as compatible with hominin features. In the 1940s and 1950s the majority of researchers gradually accepted the hominin status of australopithecines (Delisle 2007, 225-255; Gundling 2005, 101-140; Kuykendall & Štrkalj 2007).

Once the Taung child was definitively accepted as hominin - a quarter of a century after its discovery - scientists recognized that the fossil was the oldest recovered evidence for hominin evolution at the time, and was the first small-brained hominin ever described. This discovery brought about a paradigm shift in the discussion of human origins and prehistory (Kuykendall & Štrkalj 2007).

D.4.3 The hunting hypothesis

Today's perception of Dart's role in palaeoanthropological research is strongly related to his ideas that primeval man developed a taste for flesh and became hunters and cannibals, characterised by a high degree of interspecific aggression (Dart 1953; 1957; Dart & Craig 1959, 157-210).

[221] Although the Piltdown hoax was the subject of several investigations (Langdon 1992; Tobias 1992; 1993; Weiner 1955), there is, to our knowledge, no conclusive answer about the perpetrator (or perpetrators). There are different views among the historians of palaeoanthropology about the impact of Piltdown on the field. I agree with Delisle, (2000), when he concludes that during the first three decades of the 20th century Piltdown and other discoveries were easily integrated in different interpretative frameworks.

Probably the most quoted passages from Dart's texts on early hominin evolution concern his analogy between human beings and carnivores. Dart's colorful descriptions of *A. africanus* as crude, hunting, cannibalistic apes made such an impression on the contemporary scientific community that many modern authors still believe that the idea of early man as predator and killer ape was originally proposed by Dart and Robert Ardrey in the middle of the 20th century. However, such ideas had been discussed earlier by several scholars like the Scottish judge, James Burnett or Lord Monboddo (1714-1799) (Barnard 1995), the English physician Harry Campbell (†1938) and the American author and publisher Charles Morris (Cartmill 1997, 509; Stoczkowski 2002, 71-72). In 1880, with same sense of the dramatic as Dart, one author had already described primeval man as a crude creature smeared with blood when sucking bone marrow and eating raw meat and the brain of a prey (Oliveira Martins 1880). Especially detailed and still widely ignored in the palaeoanthropological literature are the ideas of Josef Müller (1894) and Carveth Read (1920). With his analogy, Dart did not start a new trend in palaeoanthropology, but followed a tradition rather popular in the early 20th century.

The American playwright and scientific writer Robert Ardrey (1908-1980) became fascinated by Dart's hunting hypothesis. He met Dart in 1955, inspected his evidence at the Johannesburg Medical School (Ardrey 1961, 28) and developed his own hypotheses on the subject in several books. With detailed accounts of Dart's palaeoanthropological ideas, Ardrey depicted early humans as social primates hunting in African open plains, stressing the role of climatic factors in the shrinking of the forests and the expansion of savannah (Ardrey 1961; 1966; 1970). Ardrey's books *African Genesis* (1961), *The Territorial Imperative* (1966), *The Social Contract* (1970) and *The Hunting Hypothesis* (1976) became worldwide best sellers and strongly influenced popular and scientific discourse on the role of hunting, climatic and environmental changes and open plains habitats in early hominin evolution. From 1972, however, Dart's and Ardrey's hunting hypotheses became the object of criticism, mainly in popular literature. This had a sensible influence in the incipient doubts on the validity of the SHs (see chapter D.6.3).

To sum up, although Dart definitely defended a SH, he cannot be regarded as the first author of this idea, as sporadically stated in historical introductions of palaeoanthropological publications. Evolutionary scenarios containing elementary arguments of modern SHs were regularly mentioned before 1925; therefore, fossil evidence found from 1924 onwards was interpreted in the light of savannah ideas already known at the time. When discussing the

alleged role of *A. africanus* in the crystallization of SH's, it is important to be aware that Dart's ideas did not have much impact in palaeoanthropological discussion immediately after the first description of *A. africanus*. This is relevant for the interpretation of the following statement by Franz Weidenreich (1873-1948) by the end of the 1930s. He, who himself vehemently rejected some aspects of the SHs, described these ideas as an already "widely spread belief" (see also Beurlen 1950, 417; Weidenreich 1939, 87-88). This popularity of the SHs was not influenced by Dart's publications on human evolution, since the acceptance of hominin status for *A. africanus* had just begun to figure in palaeoanthropology in this time, and consensus on this point was reached only many years later (see, e.g., Delisle 2007, 222-265). I regard the statement of Dart as pioneer of the SH as an insightful aspect of palaeoanthropological research – the unconsciously tendency to distort historical aspects in order to localize what is regarded as a mark stone in the history of this field – the SHs as the product of another mark stone – the discovery of the first relevant fossil evidence of early hominins in Africa. This distortion of historical facts is even more interesting when we consider the bulk of early attempts to contextualize the evolution of primeval man in open plains in the time where the Dartian ideas were or not published or not influential. Following sections will discuss different aspects of a representative choice of these ideas: the climatic determinism and interplay between analogies and climatic determinism in early open plains ideas and in alternative hypotheses.

D.5 Climatic determinism in palaeoanthropological hypotheses before the synthetic evolution

An important aspect of modern palaeoanthropological research is the use of palaeoenvironmental data to contextualize early hominin evolution. However, although some studies on the modern development of palaeoecological research in palaeoanthropology were published in the last decades (Potts 1998a; Potts 1998b; Reed 1997), the relationship between early and modern views on the influence of climatic and environmental changes in early hominin evolution are still widely ignored. It will be argued in this study that understanding this relationship is crucial for several reasons. Firstly, although early and modern palaeoecological hypotheses diverged dramatically in methodology and scientific accuracy, the arguments on the role of climatic changes in the development of key hominin features are very similar. Secondly, it will be shown that several early views proposed from the first third of the 20th century onwards on the environmental context of early hominin evolution were mostly proposed in connection with the belief that early hominins evolved in open plains.

In the last years the doubts on the origin of early hominins on savannah is regarded as the result of new palaeoenvironmental and fossil evidence. It will be shown that this view has to be put in a relative perspective.

D.5.1 Cradles of mankind: climatic and environmental changes in different continents and time periods

The idea that climate has a strong influence on living organisms was already widespread in pre-Darwinian times. The scientific requirement for a systematic research on the influence of climate on humans led to the foundation of anthropogeography or human geography. The origin of this field strong relates to the work of the German naturalists Alexander von Humboldt (1869) and Friedrich Ratzel (1882); see also Scherer (1830, 57) and Baer (1874, 519). And although at the end of the 19th century Ratzel sounded a note of caution concerning the widespread speculations being made of a strong climatic influence on human evolution (Ratzel 1882, 298) (see also Hesse (1924, 105)), this was out of step with the zeitgeist which stressed the role of environment in the evolution of organisms connected to a simple scenario for hominin evolution - a view compatible both with neo-Lamarckian and Darwinian concepts.

Darwin expressed many thoughts on the relationship between climate and natural selection in his book *Origin of Species* (1859) and the possible effect of climatic changes on human races in a chapter in the *The Descent of Man* (1871, see, e.g., vol. 1, chapter 4), but devoted just a few words on the possible role of environmental change on the origin of a bipedal primeval man. Beside the passage (quoted above, chapter D.3.1) of a progenitor of man becoming less arboreal and bipedal "owing to a change in its manner of procuring subsistence, *or to some change in the surrounding conditions*" (Darwin 1871, vol. 1, 140, italics added), he wrote in the same work:

> If then the ape-like progenitors of man which inhabited any district, especially one *undergoing some change in its conditions*, were divided into two equal bodies, the one half which included all the individuals best adapted by their powers of movement for gaining subsistence or for defending themselves, would on an average survive in greater number and procreate more offspring than the other and less well endowed half. (Darwin 1871, vol. 1, 136, italics added)

Here, Darwin is conservative in the use of global climatic changes to contextualize primeval man. However, this precaution changed radically in the decades following the *Descent of Man*. In the 11th edition of his *Natürliche Schöpfungs-Geschichte* Ernst Haeckel wrote about

the cooling process in the Tertiary age and the theoretical influence on living organisms, which were obliged to adapt to or to escape from the cold (Haeckel 1909b, vol. 1, 330). He also speculated about the role of cooling conditions on the biological diversity in the Ice Ages (Haeckel 1909b, vol. 1, 331). At the time, the climatic changes in the Ice Ages became one of the most important topics in geology and climatology. And although these events occurred too late to be included in the discussion on the emergence of early hominins, many authors were not able to overcome the temptation to see the Ice Ages as crucial in early hominin evolution. In late 19th and early 20th centuries, students of human evolution began to envision evolutionary scenarios in which primeval man was strongly influenced by climatic and environmental changes. Primeval man began to be depicted as a miniature piece on a giant chess board, subordinate to the inexorable forces exerted by geological and climatic events.

Climatic and environmental changes are obviously not restricted to single regions of the planet. Consequently, there were few places on earth that were not considered suitable for the emergence of primeval man.[222] In the early 20th century, contrary to the above mentioned Darwin's views suggesting Africa as the most probable cradle of mankind (Darwin 1871, vol. 1, 199), East and Central Asia with the impressive Tibetan highlands and vast open plains became a popular place to contextualise primeval man's evolution (Bowler 1986, 173-185; Dennell 2001).

It is difficult to assess to what extent various factors influenced the views on Asia as the location of human evolution in the first half of the 20th century. From today's point of view it is tempting to regard fossil discoveries as the main factor in establishing this idea.[223] However, this view is problematic when confronted with historical facts. Above all, it ignores the wide spectrum of influential discussions in the 18th and early 19th century in which Asia was seen as the place where certain races (Banton 1987; Graves Jr 2008; Poliakov 1977,

[222] To cite a few examples: in Europe and North Asia (Müller 1894; Wagner 1889, 162-174); in the northwestern part of Europe (Wilser 1910, 55); in northern or central Europe (Koch 1929, 63); in Australia (or in a sunken land close to Australia) (Klaatsch 1922, 91-92; Knauer 1916; Müller de la Fuente 1906; Schoetensack 1901) ; in Africa (Darwin 1871, vol. 1, 199) or in a "warm continent or large island, such as Australia or New Guinea, or Borneo" (Darwin 1871, vol. 1, 157); in the North Pole (Biedenkapp 1906); in South America by Florentino Ammegnio (see Podgorny 2005); different human origins in different parts of the world, implied in the views of Giuseppe Sergi (1913, 150-152), Carl Vogt (1863, vol. I, 285) and Maurus Horst (1913, 21-22); somewhere in the northern part of an early EuroAfrican continent (Brinton 1886); in South Asia, or in Africa, or in the hypothetical sunken continent Lemuria (Haeckel 1909a, vol. 2, 755-757); in South Asia, but for other reasons as then proposed by Haeckel (Zimmermann 1903). Several other proponents of Asia as the cradle of mankind are mentioned in chapter D.6.1.

[223] The most relevant of these discoveries was *Pithecanthropus erectus* (today *Homo erectus*) by the palaeoanthropologist Eugène Dubois (1858-1940) in 1891 and 1892 at Trinil, in central Java and the subsequent research by the palaeontologist and geologist Gustav H. R. von Koenigswald (1902-1982) from 1931 to 1941 (see Tobias 1984b).

205ff), certain languages (Borst 1995b) or the whole of mankind originated.[224] These discussions were, of course, carried out in the complete absence of hominin fossil material. In German-speaking countries, Immanuel Kant (1982 [1775], 23) and especially Johann Gottfried von Herder (1852 [1784-1791), vo. 28, 393-414) eloquently defended a positioning of mankind's childhood in Asia. Early concepts of Tibet as the cradle of mankind were also influential in the development of racist "evolutionary" ideas from theosophists, which were adopted among others by sympathisers of Nazi ideology and are still present in neo-Nazi discourses today (Brauen 2000, 36-93).

In early 20th century, scientists increasingly used arguments on climatic and environmental changes to corroborate their views on Asia as the location of human evolution (see also chapter D.6.1). For instance, the palaeogeographer Theodor Arldt (1878-1960) provided explanations based on geological causes for the cooling of climates in the Pliocene (Arldt 1907a; Arldt 1907b). Arldt stressed the harsh-conditions of an isolated Tibetan territory with sparse vegetation and "a deteriorating climate" in the Pliocene as crucial factors in the transition from ape-man to man (Arldt 1907a, 606). In another work he explained that Africa or other tropical areas are not acceptable places for the cradle of mankind, since we should expect a certain state of emergency for the evolution of primeval man (Arldt 1907b, 211). He provided explanations about the geological causes for the cooling of climates in this time – a massive rise of Tibetan highlands (Arldt 1907b, 212).

Very similar views were expressed in 1944 by the German-American palaeontologist Amadeus W. Grabau (1870-1946) in a manuscript published posthumously in 1961. He also regarded Tibet as the cradle of mankind and the emergence of primeval man as strongly influenced by geological events with subsequent environmental changes. Especially interesting for the present discussion is his opinion on the causes of the split between apes and primeval man:

> The only conceivable change that would bring about this new condition is the disappearance of the forests themselves. Instead of the apes leaving the trees, the trees left the apes. Then, when the trees were gone and no escape from the tree-less area was possible, it became a struggle to continue under such new conditions, a struggle for existence, where survivors would be few, while those that were doomed to extinction, because they were incapable of adaptation, formed the majority. (Grabau 1961, 158)

[224] The German prefix "Ur-" reflects this early vivid interest in the origin (*Ursprung*) of language (*Ursprache*), primordial people (*Urvolk*), primeval man (*Urmensch*) or an early form of civilization (*Urzivilisation*).

By depicting primeval man as a passive participant in climatic and environmental changes, the picture of "trees leaving the apes instead of apes leaving the trees" became the most important element of the modern SHs. The same basic picture was used by other authors, especially by Hans Weinert (see chapter D.5.2).

An early and influential view of climatic determinism in palaeoanthropology was defended by the German naturalist Moriz (or Moritz) Wagner (1813-1887), who is today known for his ideas on the role of migration and isolation on the origin of species (Wagner 1889). In a posthumously published work[225], Wagner criticised Darwin's views on the cradle of mankind in Africa in a chapter entitled *Ursprung und Heimat des Urmenschen* (origin and home of primeval man) (Wagner 1889, 162-174). He argued that Europe, during the middle of the Miocene, was too warm and the environment too opulent and paradisiacal to give the initial impulse to the evolution of primeval man (1889, 169-170). Such an environment, wrote Wagner, would not promote the development of "stupid simian quadruped" (*dummer affenartiger Vierhänder*) (Wagner 1889, 166) . For similar reasons he did not believe in Africa as cradle of mankind. He wrote:

> The African climate never lost its warm character; the African soil never lost the evergreen fruit-trees. Cold, privation and hunger never happen in the home of chimpanzee and gorilla, and never forced pithecoid creatures to come down from their trees, to modify their movements, posture and locomotion, to enable them to sharp the edges of stones and so be able to kill other creatures. (1889, 166, my translation)

Why, continued Wagner (1889, 170), should the apes voluntarily leave paradisiacal Africa and migrate to the cold Europe, where the environment was much harsher and the struggle for life was much harsher? Additionally, neither fossil anthropoids from the Tertiary nor rudimentary stone tools from African sediments or caves from the Pleistocene were found; instead, this evidence was discovered in Asia and Europe. Wagner assumed therefore, that the origin of man occurred in the northern part of the Old World (Europe or North Asia) in a time of strong climatic changes, i.e., in the Pleistocene. He saw a clear connection between the cooling of temperature in the Ice Age and the reduction of vegetarian food in the place where quadrumane *Dryopithecus* lived. These in Wagner's view pre-human primates were forced to live in the treeless rocky landscapes in the Palaearctic region and had to give up their fruit diet

[225] According to Wagner (1889, 117), this essay was first published in the journal "Das Ausland" in 1871 (issues 13-15, 23 and 24, 37-40, 45 and 46); I did not consult this edition. The same work was posthumously published under the title *Die Entstehung der Arten durch räumliche Sonderung* (Wagner 1889); I am quoting from this work.

and climbing technique to gradually adopt an upright posture. In their struggle against starvation, this species was transformed from "stupid anthropoids" (*stupiden Anthropoiden*) into a permanent biped, intelligent and carnivorous "Anthropos", able to use stones as tools to hunt (1889, 166-174).

In many senses, Wagner's Palaeartic hypothesis represents the beginning of a new era in the history of palaeoanthropology. As far as can be assessed, he was the first author to depict early human evolution as the result of climatic and environmental changes. Additionally, he was the first author to discuss extensively the role of geographic isolation and migration in speciation process, using this approach to formulate scenarios on early human evolution. Wagner's views on the origin of man were influential on German-speaking authors. Although some authors around 1900 explicitly mentioned him (Hoernes 1909, vol. 1, 212; Müller 1894; Zimmermann 1903), later authors often preferred to borrow his views without acknowledging Wagner's work (see, e.g., Weinert's ideas on chapter D.5.2).

Among the works which acknowledged Wagner, the most interesting is an essay entitled *Über Ursprung und Heimat des Urmenschen* (On the origin and home of primeval man) published by Josef Müller in 1894. The great similarity to the title of Wagner's chapter on human evolution was intentional: Müller took up most of Wagner's Palaeartic hypothesis and complemented it with own views (Müller 1894). Fascinated by Wagner's arguments of human beings formed through harsh climatic and environmental conditions, Müller was convinced that Wagner's work on human evolution belonged to the "most important and interesting publications in Darwinian literature" (Müller 1894, 3, my translation). However, according to Müller, Wagner's short chapter remained almost unnoticed, as it was published in the same work where Wagner presented his influential essays on migration and speciation (Müller 1894, 3). Like Wagner, Müller saw the Ice Age (*Eiszeit*) as crucial for the origin of primeval man, and like Wagner he placed this development in the "northern slope of the great Asiatic or European mountains" (1894, 31). Again under a strong consideration of Wagner's ideas, Müller regarded primeval man as a predator and carnivore creature, explaining this evolutionary novelty as a response to a harsh environment. He was concerned with the fact that primeval man, as a highly specialised arboreal species, would be very inferior in his incipient terrestrial locomotion. Differently to the view expressed by other authors at this time that depicted the passage from trees to open plains as self-evident and unproblematic,[226]

[226]This was for instance the case in Lamarck's and in (one of) Darwin's open plains scenario. Later authors often depicted early humans' interaction with predators as salutary. For instance, the German psychiatrist and

Müller believed that these arboreal adaptations would be an enormous handicap in primeval man's attempts to hunt other animals or to defend against predators. He saw the solution for this problem in the incipient use of tools by primeval man; on this topic Müller added several details to Wagner's hypothesis. For instance, he argued that an intelligent progenitor of man would be able to use stones as long-range weapons (*Fernwaffen*) for hunting and for defence (1894, 23-29). He related this behaviour to the origin of bipedalism (1894, 37-44). Müller believed that the first humans were "cliff-apes" (*Felsenaffen*): a such a rocky environment was, in his opinion, crucial for human evolution, as primeval man would have the possibility to escape from predators and have a great supply of rocks to use as weapons (1894, 32). He envisaged a "didactic scenario" to explain the use of weapons: cliff-apes pursued by a predator witnessed how stones rolling from the slopes accidentally killed or hurt the predator. This accident exchanged the roles, and the predator becomes a prey. This often repeated experience led to a regular use of stones as weapons (e.g., rolling stones from the slopes to kill other animals) which, after a long period of time, led to a skilled use of stones as long-range weapons (1894, 35). He mentioned "today baboon and other monkeys" [*der heutige Pavian und andere Affen*] as analogous creatures, exploring a cliff-environment (1894, 32).

In the first third of the 20th century very similar views were suggested by two other authors: Suschkin and Abel. In a posthumous paper published 1933[227], the Russian ornithologist Peter Petrowitsch Suschkin (1868-1928) complained that the ecological aspects of the evolution of human beings were pretty neglected. After a lengthy analysis of the distribution of the fauna in highlands of the earth he concluded that the ancestors of humans lived in Central Asia – and he mentioned Matthew and Osborn as the main propagators of this idea. Similarly to Wagner and Müller, he regarded the bipedalism of primeval man as an adaptation to a life in a landscape with rocks and open plains; a similar environment as explored today by baboons (Suschkin 1933, 300). In his scenario, primeval man evolved under the influence of rough climates (Suschkin 1933, 304). He defended a version of Lamarck's tower-hypothesis to explain the reason for the development of bipedalism: by an erect posture primeval man would be able to identify friends and enemies from the distance (Suschkin 1933, 300). The helplessness of primeval man was essential to the development of his intellect (Suschkin

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sociologist Franz Müller-Lyer (1857-1916) wrote in 1911 (here quoted from an edition from 1948) that human arboreal ancestors lived in a kind of refuge (*Asyl*), where the food grew practically in their mouths, and turned into "warriors and hunters" (*Krieger und Jäger*) when they began to adapt to a terrestrial life. He described the big predators of primeval man as "prehistoric educators" (*Erzieher der Urzeit*) (Müller-Lyer 1948, 48-49).

[227] Suschkin noted that his ideas on human evolution were already published before (see also Stresemann 1929; Suschkin 1933).

1933, 301-302). He saw *Australopithecus africanus* as a failed attempt at hominisation (Suschkin 1933, 296). Perhaps, according to Suschkin, the climates in South Africa were not rough enough, or perhaps the massif was not high enough (Suschkin 1933, 304). In his first hypotheses on human evolution, the Austrian palaeontologist Othenio Abel (1875-1946) also defended a classical view of the SH in connection with climatic changes. Innitially he regarded Central Asia as the cradle of mankind (Abel 1919). Later (1931, 379-380), he considered the possibility that the bipedalism of the first hominins evolved in a phase when they lived as cliff-dwelling climbers (see also Ehrenberg 1949).

D.5.2 Climatic determinism in early savannah hypotheses: Ludwig Reinhardt, Gustav Steinmann and Hans Weinert

Especially impressive for an emphasis of climatic determinism are the hypotheses proposed by the Swiss author Ludwig Reinhardt. He saw as possible that the first steps in human evolution occurred in the Oligocene, perhaps on a continental island[228], in a scenario with sparse vegetation (Reinhardt 1906, 6-7). He regarded it as crucial that the origin of primeval man did not take place in a paradise environment, but in an area with less favorable conditions. In this harsh environment the struggle of life was stronger, selecting the best of our ancestors (Reinhardt 1906, 6). Reinhardt saw the climate as the driving force of human evolution, by explaining the origin of bipedalism in connection with climatic change and the dwindling of forest areas when the ancestor of man was forced to walk from one tree to other (Reinhardt 1906, 7-8). He used Lamarck's tower hypothesis to explain the origin of bipedalism: the upright posture allowed primeval man to see further over the plains to search for prey or enemies (Reinhardt 1906, 8), and to have free hands to carry weapons or tools (Reinhardt 1906, 8-9). Reinhardt was one of the first authors in the 20th century to develop Wagner's and Müller's concept of a climatic determinism responsible for the emergence of primeval man, and he was also a pioneer in stressing climatic factors in connection with the emergence of open plains.

Some interesting thoughts on climatic determinism in the evolution of primeval man had already been expressed by the German geologist and palaeontologist Gustav Steinmann (1856-1929) in his book *Die geologischen Grundlagen der Abstammungslehre* (Steinmann 1908). Steinmann wrote about the causes driving human ancestors to abandon the primordial quadrupedal locomotion, using climatic determinist arguments in connection with modern sounding open plains ideas. He envisaged a pithecoid creature, with a similar quadruped

[228] See chapter D.3.1 above on the island hypothesis by Herschel and Darwin.

locomotion as today's apes living in forests; climatic changes had gradually thinned the forests and transformed them into savannah regions. According to him, the arboreal ancestors of humans were then forced to adapt to the modified conditions and occasionally adopt an upright or semi-upright posture, similar to today's apes. Only few modifications of these intermediate stages, affirmed Steinmann, would be necessary for the adoption of a permanent bipedalism (Steinmann 1908, 266). With some irrelevant adaptations in the vocabulary, Steinmann's open plains ideas would fit perfectly into a palaeoanthropological work of the late 1990s.

Steinmann saw all further modifications as a consequence of this crucial phase in early human evolution, especially the increased development of the senses, the evolution of hands to a versatile organ and (as a result of both modifications) the increased mental faculties and brain mass. He also had an explanation for the alleged fact that a decrease in forest area was beneficial for the evolution of human beings, but not for apes:

> We can imagine the geographic area of such pithecoids being occupied by different closely related species, which we might fuse in a systematic sense into a "genus", and that this area would be affected by a climatic change in the sense described above. In that case, some species living close to river plains or in very humid areas would retreat into their original environment, keeping their previous habits; in contrast, other species living close to the timber line would adopt a bipedal locomotion and so gradually be able to occupy the newly formed and already present savannah and brushwood areas. (Steinmann 1908, 266, my translation)

Despite the inclusion of climatic and environmental changes as crucial factors in early human evolution, several arguments proposed by Steinmann are quite similar to Lamarck's ideas, especially Steinmann's general scenario of primeval man abandoning the forest and adapting to open plains which is basically the same as proposed by Lamarck. Furthermore, Steinmann's explicit statement on other primate species being forced to retreat into their original environment, and keeping their previous habits (Steinmann 1908, 266) is coincident with Lamarck's view of a primeval man banishing other primates "into forests or other desert places" (Lamarck 2006, 170). Perhaps more revealing than mere coincidence in primeval man evolutionary scenarios, are Steinmann's speculations on vertebrates' evolution. He argued that giraffes are descendant from aquatic dinosaurs and dolphins are descendant from *Ichthyosaurus* (Steinmann 1908, 278-279). Although Steinmann was not the only scholar in the early 20th century who went beyond reasonable boundaries with speculations on evolution, his interpretation of vertebrate phylogeny was an incredible *faux pas* for a

professional palaeontologist in this time.[229] However, if one considers that Steinmann's ideas were the product of an uncritical assimilation of Lamarck's views, perhaps his error is understandable. In his *Philosophie zoologique*, Lamarck erroneously suggested that birds descended from turtles, amphibian mammals from crocodiles, monotremes from penguins, and ruminants and pachyderms from animals living close to the shore (like walruses and manatees) (Lamarck 1994, 646-647). All indications are that Steinmann could not resist attempting to enlarge Lamarck's original list with further aquatic counterparts to terrestrial vertebrates. He did it without considering the accumulated evidence showing that several aquatic animals are not *primarily* aquatic, but descend from terrestrial animals and therefore are *secondarily* aquatic. The strong similarities between Steinmann's and Lamarck's views can hardly be regarded as coincident, since Steinmann was an ardent proponent of Neo-Lamarckism, often quoted Lamarck and even dedicated his *Grundlagen* to him.

Curiously, in their general statements on the evolutionary path of living organisms, Lamarck and Steinmann were much closer to the views proposed by the French diplomat Benoît De Maillet (1656-1738) in the manuscript *Telliamed*. As shown in Appendix B, although the idea of aquatic counterparts was sometimes expressed by 18th century naturalists, De Maillet was the first author who tried to identify such counterparts in the framework of a detailed evolutionary concept.

In the first half of 20th century, in the attempts to justify why the occupation of open plains should promote primeval man's evolution, some authors began to defend two very peculiar views of the role of environment on the emergence of the first upright ancestors of humans: on one hand, as already explained, the contrasting representation of forests as a place of stagnation and open plains as a place of development, on the other hand, the idea of "trees leaving the apes" instead of "the apes leaving the trees". As naïve as they perhaps sound today, these views became an essential part of the SHs defended in the last 100 years. This idea was repeatedly propagated by the influential German anthropologist Hans Weinert (1887-1967) in several scientific and popular works in the 1930s and 1940s: the ancestor of primeval man, according to Weinert, did not come down from the trees; instead, "the trees went out from under the ape, thus putting him on the ground whether he wanted it or not" (Weinert 1932, 339, my translation). Weinert frequently stressed the alleged difference between a paradisiacal life in the forest and the hard conditions on the open plains, for

[229] The negative remarks should not be used to denounce Steinmann's whole scientific career; he was seen at that time as a hardworking and competent geologist (Pfannenstiel 1957). See also the ideas expressed by Dieterici in Appendix A, chapter A.4).

instance in 1940: "[…] the *dolce far niente* of a tropic or subtropic forest life with abundant food did not exist anymore" (Weinert 1940, 72, my translation). One year later, he stated that "The forest was in any case not a place appropriate for the emergence of man. Then man emerged not in a paradise; he appeared because the paradise disappeared" (Weinert 1941, 48, my translation).

Several of Weinert's statements on the origin of primeval man strongly recall Moriz Wagner's and Josef Müller's ideas on the influence of the cooling in the Ice Age (see above, chapter D.5.1). Similarly, Weinert's repeated allusions to the paradisiacal and delightful life of pre-humans and an awkward primeval man's incipient attempts to walk on the ground are almost identical to Wagner's and Müller's formulations. Although Weinert did not acknowledge Wagner's or Müller's works as sources for his specific open plains ideas, at least one sentence clearly links Weinert to these authors in one of his books. Weinert wrote: "It was once said: 'Without an Ice Age, no man' [*Ohne Eiszeit kein Mensch*], today we say even more clearly: 'Through the Ice Age, the man' [*Durch die Eiszeit der Mensch*] (Weinert 1932, 352, my translation). The first sentence is attributed to Moriz Wagner[230]; Joseph Müller used it as an epigram for his work on human evolution (Müller 1894, 3).

D.6 Interplay between analogies and climatic forcing models

In palaeoanthropology, several models of early hominin evolution are based on analogical reasoning. In these hypotheses, alleged convergences between hominins and other organisms are identified and used to infer early hominin adaptations to a certain environment. The rationale for certain comparisons formulated within traditional hypotheses can be described as follows: taking into consideration that environmental changes are a crucial factor in the evolution of terrestrial organisms, it is reasonable to assume that human ancestors are not the only organisms that were forced (by climatic and subsequent environmental changes) to abandon a particular environment A and to adapt to a different environment B. Therefore, it should be possible to identify such organisms, understand the circumstances in which they evolved and use this information to explain critical phases in primeval man's evolution.

[230] I did not find this information in Wagner's works that I consulted. However, in his biographical sketch of Moriz Wagner, Karl von Scherzer wrote: „Ohne Eiszeit kein Mensch! Das war sein naturphilosophisches Dogma" (Without an Ice Age, no man! This was his natural-philosophical dogma) (Scherzer in Wagner 1889, 27). Maurus Horst also attributed this sentence to Wagner. He regarded him as the first scientist who recognised the importance of climatic change in the northern hemisphere as a factor of progress [*Fortbildungsursache*] in early human evolution; furthermore, he mentioned, among others, the works of Josef Müller, Theodor Arldt and Ludwig Reinhard in this context (Horst 1913, 17). Usually, this sentence is attributed to Weinert (see, e.g., Overhage 1959b, 14, and Boné quoted by Overhage).

Although single analogies played a crucial role in palaeoanthropology, it is surprising that these comparisons were not investigated in detail. Such an analysis is important for different reasons. On one hand, since analogies are often used in the reconstruction of the evolutionary past of other organisms, it is possible to compare analogical reasoning in other biological fields with the analogies used in palaeoanthropology. On the other hand, several analogies are very persistent, and in slightly modified form they are still defended in modern palaeoanthropological discussions. Even such topics which are usually regarded as intrinsically related to modern investigations (like the use of baboons as referential models or the use of global climatic changes in connection with models based on analogy) were often formulated and extensively discussed in the early literature. Several of these ideas are unknown to modern palaeoanthropologists or historians of palaeoanthropology, as they were often propagated by German-speaking scientists, who, despite the fundamental role that they played in the formulation of evolutionary and palaeoanthropological hypotheses in late 19th and early 20th century, are nevertheless under-represented in most[231] investigations of the history of this field. The exceptions concern those authors who participated in the early discovery and interpretation of fossil evidence of Neanderthals, as for instance by Gustav Schwalbe and Hermann Klaatsch, or the ideas on human origin proposed by the German Darwinian Ernst Haeckel. However, even the earlier analogies proposed by known English speaking scientists (as for instance Henry F. Osborn, William D. Matthew and Joseph Barrell) are often overlooked in historical investigations. For a discussion on other analogies in palaeoanthropological hypotheses see chapter 6 in the main thesis.

D.6.1 Kangaroos, horses, first terrestrial vertebrates: analogies in early and modern savannah hypotheses

One of the most impressive examples of the use of analogies in an early hypotheses[232] on the origin of primeval man is supplied by the German zoologist Max Hilzheimer (1877-1946) in a paper entitled *Aphoristische Gedanken über einen Zusammenhang zwischen Erdgeschichte, Biologie, Menschheitsgeschichte und Kulturgeschichte* (Hilzheimer 1921). Hilzheimer explicitly considered forests as "place of stagnation" and open plains as "place of development" in the evolution of man[233] and other organisms. He was convinced that the

[231] The Jesuit, anthropologist and biologist Paul Overhage is one of the few authors who included several German-speaking authors in his historical investigations (see, e.g., Overhage 1959a). See also Bender (1999a)

[232] The baboons-analogies proposed by Josef Müller, Peter Suschkin and Othenio Abel were treated in connection with incipient ideas on climatic determinism (see chapter D.5). Some thoughts on climatic changes in connection with concept of race in the Third Reich were expressed by Hutton (2005).

[233] Hilzheimer did not focus only on the possible causes of the split between humans from pithecoid ancestors, but did not hesitate to use this formula to justify farfetched ideas on the role of landscape in the divergence

evolution of most terrestrial animals was mainly influenced by the expansion or reduction of wooded areas. His belief in arboreal apes as a "failure of natural experiments" was the starting point of a highly anthropocentric categorisation of "stagnated forest fauna" and "progressive open plains fauna". He discussed in detail how forest reptiles and mammals are "less developed" than their counterparts living on open plains, without offering any reasonable criteria for this discrimination. Very similar to Lamarck, he saw the emergence of bipedalism in connection with the ability to scrutinise the open plains. He regarded kangaroos (because they are, like humans, adapted to open plains and able to move on their hind legs) as "the most developed marsupials" (*die höchststehendsten Beuteltiere*) and used them in an analogy with humans (Hilzheimer 1921, 187). Like other early authors, he saw the forest as a comfortable place, radically different from the open plains, which he regarded as a rough environment, characterised by strong contrasts and hard interspecific competition (Hilzheimer 1921, 189-190). But why should primeval man abandon the forest paradise? He did not. Like Hans Weinert some years later, Hilzheimer viewed it as probable that the human ancestors did not leave the forest, but the forest landscape transformed gradually and imperceptibly into open plains (Hilzheimer 1921, 194). Hilzheimer's ideas exemplify the degree of oversimplification implicit in several early theoretical concepts of early human habitats. This oversimplification reflects the need to conceive a landscape where hypothetical human ancestors could exist and behave according to the premises of the specific hypotheses; on idealistic zonation see chapter 3.4 in the main thesis.

Analogies using other organisms to illuminate still obscure phases in primeval man's evolution were characterised not only by simplistic and anthropocentric views of the evolutionary processes; they also assumed misguided ideas whereby organisms are driven to a continuous and linear evolutionary progress towards more complex forms. Such reasoning can be recognised in the ideas presented by the geologist Joseph Barrell (1869-1919), when he proposed an analogy between alleged similar evolutionary processes relevant for the emergence of primeval man and the emergence of the first land vertebrates (Barrell 1916; 1917). Strongly influenced by William Diller Matthew's[234] ideas, Barrell was convinced that the evolution of human beings took place in Central Asia and was directly connected to climatic changes in the past. He believed that recurrent epochs of semi-aridity brought

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between human races or nations. He believed for instance that the effect of climatic and environmental changes could explain why anti-Semitic tendencies are present only in Germany but not in other European countries (Hilzheimer 1921, 205). For more details see please the original.

[234] See references to Matthew's *Climate and Evolution*, (Matthew 1950) [first published 1915] in Barrell (1917, 17, 20).

conditions that severely suppressed river fish habitats (Barrell 1916, 502; 1917, 17). With increasing aridity, the rivers were reduced in flow, the content of oxygen decreased and fish were isolated in pools, stagnant and foul from the decomposition of animal and plant remains. From primitive fish (under the constraints of severe semi-aridity of the Devonian period) emerged the amphibians, able to carry forward their activities as terrestrial animals (Barrell 1916). Barrell stressed the key role of environmental changes and natural selection in evolutionary events: "Natural selection, although discredited as a cause determining specific variations, appears nevertheless to be a major factor in evolution, the driving cause in association with changes in environment, which has forced the great advances in organic progress" (Barrell 1916, 504). These ideas, as he stated, gave him the inspiration for a new scenario on the evolution of primeval man (Barrell 1916, 502-503; 1917, 17). In the paper *Probable relations of climatic change to the origin of the tertiary ape-man,* after summarising his hypotheses on the rise of air-breathing, he defended the idea that an analogous process of climatic events and natural selection was responsible for the emergence of the first upright human ancestors:

> Did a similar climatic change in the Tertiary period acting on a species of large-brained and progressive anthropoid apes isolated from the regions of continued forest compel them to adapt themselves to a terrestrial life or die? Did the gradual dwindling, leading even to the extermination of forests, in a region from which the forest fauna could not escape, produce a rigorous natural selection which transformed an ape, largely arboreal and frugivorous in habits, into a powerful, terrestrial, bipedal primate, largely carnivorous in habit, banding together in the struggle for existence and by that means achieving success in chase and war? (Barrell 1917,17)

He was convinced that many of the specific elements that contributed to the evolution of early land vertebrates were also crucial in the evolution of man. He mentioned the alleged influence of a semi-arid climate as the most important factor in this evolutionary scenario:

> The gradual elimination, first of food of the forests, lastly of the refuge of the trees, through increasing semi-aridity, would have been a compelling cause as compelled as mandatory as the semi-aridity which compelled the emergence of vertebrates from the waters, transforming fishes into amphibians; the first of the vertebrate rulers of the land. It is the purpose of the present article to assemble the evidence which suggests this climatic cause acting upon our simian ancestors as a controlling factor in this latest of the major stages in human evolution. (Barrell 1917, 17)

According to Barrell, the primary cause for the differentiation of ape-men from the apes was "the compulsion of increasing aridity in Miocene times, by isolating anthropoids north of the Asiatic mountain systems and reducing the forests there to savannahs and open plains" (Barrell 1917, 19). He speculated about the predatory activities of early man living in open plains: "With the use of crude weapons for the killing of animals the modifications in teeth and jaws represent a carnivorous-omnivorous adaptation fully worked out in a terrestrial and predatory primate" (Barrell 1917, 22). Barrell asked why a species of ape would choose a more hazardous life voluntarily. The answer to this question has strong similarities to Arldt's speculations (see chapter D.5.1), published ten years earlier: that human ancestors were obliged to leave the trees (Barrell 1917, 23).

A similar analogy was presented by the American palaeontologist Richard Swan Lull (1867-1957) in his book *Organic Evolution* (1917). The similarity is probably not a coincidence, as Barrell acknowledged his debt to Matthew and to Lull (Barrell 1917, 17). Lull believed that the drying up of central Asia in Miocene and late Pliocene times forced pre-human ancestors to descend from the trees, "a step which was absolutely essential to further human development" (Lull 1917, 672). Like Barrell, he drew a comparison with the evolution of the first terrestrial vertebrates: as the lakes and ponds of the Devonian had gradually dried up with the increased aridity, the primitive amphibians were forced to move across dry land. Analogous to this scenario, the ancestors of mankind had been forced to migrate from one shrinking patch of forest to another, until some groups of survivors were fully adapted to live permanently on the open plains (Lull 1917, 672). Of interest in this analogy (already clearly formulated by another author (Reinhardt 1906, 7)) is that the tree-to-tree scenario has been essential in the hypotheses formulated by many scholars after the modern evolutionary synthesis. Ideas similar to Lull's analogy were later used by influential scientists like Ellsworth Huntington[235] (1945, 26), Gerhard Heberer (1959, 1131) and Wilfrid E. Le Gros Clark (1978, 187). The tree-to-tree scenario belongs to the most influential versions of the savannah hypotheses in modern palaeoanthropology.

[235] Huntington's primary concern was the corroboration of his thesis of the intellectual superiority of some human races (Huntington 1918, 147-148), and that the climatic factors are the crucial factors for this racial superiority (Huntington 1918, 148), see Martin (1973). A detailed exposition of his ideas was published in his book *Mainsprings of Civilizations* (Huntington 1945). As his theories concerned mainly the development of recent races of human being, the importance of his work is more related to the role of new methods and work programmes in anthropology. Especially his book *Civilization and Climate* (3rd ed. Huntington 1924) had a perceptible influence on many authors, even on German-speaking scientists in the 1920s, such as for instance Konrad Olbricht (1923) and Egon Freiherr von Eickstedt (1925).

A further popular form to corroborate scenarios of early human evolution was the direct comparison between humans and animals living on open plains, as the peculiar analogies between the evolution of man and horses. The term "peculiar" is appropriate here, since such analogies cannot be corroborated by any anatomical or physiological convergences between these organisms, but were mainly motivated by two ideas. On one hand, the fossil record of early horses was excellent in the late 19th century, and some scientists viewed it as natural to compare this material with the very scarce hominin fossil evidence of this time. For instance, the quality of equid fossil material inspired the British science writer Samuel Laing (1812-1897) to compare the evolution of horses with the evolution of man to help clarify aspects related to time of emergence and tempo of evolution of both organism groups:

> The horse, whose ancestral pedigree is the best established of any of the existing mammals, was already in existence in the Pliocene period, and the Hipparion, which is the first of the links connecting him with the primitive mammal, is first found in the Miocene and not later than the Pliocene. Why should the development of man have begun later, and followed a more rapid course that that of the horse? (Laing 1893, 160)

On the other hand, reflecting the admiration of horses as magnificent and noble animals, several scholars in the past believed that they must have evolved in a similar way to our own species (note the anthropocentric view implicit in this analogy). Finally, the fossil evidence allowed a clear picture of the phylogeny of modern horses. The evolutionary history of this group became one of the most important examples of a gradual transition in vertebrates in late 19th century. It is therefore not surprising that horses were used as referential animals in the reconstruction of human past, especially by North American palaeontologists who were specialised or at least interested in Equidae evolution.

An early human-horse analogy was proposed by William Diller Matthew (1871-1930), probably the most influential scientist in the fields of vertebrate palaeontology and zoogeography of his time (Colbert 1992; Rainger 1997, 648-649). Influenced by the ideas of Alfred Russel Wallace on zoogeography (Wallace 1876; Wallace 1898) and by the ideas on climatic fluctuations proposed by the American geologist Thomas C. Chamberlin[236], Matthew developed his own views on the dispersal of vertebrates which were summarised in his most influential book *Climate and Evolution*[237] (1st ed. 1915, here quoted from Matthew 1950). He

[236] Chamberlin's theories involve an alteration of climates through the course of geological time from extremes of warm, moist tropical and uniform, to extremes of cold, arid zonal climates (Chamberlin 1897; 1898; 1899)
[237] According to Matthew (1950, 3), he gave a talk upon "Climate and Evolution" before the Linnaean Society in 14 January 1902.

saw the numerous hypothetical land bridges connecting continents separated by deep oceans as unnecessary to explain geographic distribution of vertebrates. Matthew believed that in "in a broad way the present distribution of land and shallow water on the one hand, of deep water on the other, has been substantially unchanged" (Matthew 1950, 4). He adopted the theory of isostasy – a term first proposed by Clarence Dutton (1889)) which states that continents and oceans are held in balance (Matthew 1950, 4). He believed, therefore, that although some occasional great changes of level have occurred in the past, they were probably of restricted extent and not essential for the general configurations of the continental platforms (Matthew 1950, 20). On the zoogeographic side he explained the pattern of distribution of vertebrates, among others, through "natural rafts"[238], through his hypotheses on "centres of dispersal" and – similar to other authors before him[239] – through an oversimplified thesis on evolutionary development shaped by climatic and environmental changes. Using a north polar projection to explain the dispersal and distribution of every group of vertebrates, he argued that vertebrates had often originated in the climatically more challenging northern zones, the Holarctic, and then dispersed in waves to more favourable areas in the Southern Hemisphere. By transferring Chamberlin's theories on the vertebrate palaeontology, Matthew explained that the periods of arid and markedly zonal climate "would be unfavorable to abundance of life and the ease with which animals could obtain a living" (Matthew 1950, 7). In these periods, stated Matthew, the animals must maintain themselves against the harsh conditions of nature such as the scarcity of food, variations of temperature, and higher concurrence with other organisms. In the moist tropical phase it would be the opposite: abundant food, constant temperature and less concurrence (Matthew 1950, 7). "We should expect", he wrote, "to find in the land life adapted to the arid climatic phase a greater activity and higher development of life, special adaptations to resist violent changes in temperature and specializations fitting them to the open grassy plains and desert life" (Matthew 1950, 7).

He saw it as evident that human beings emerged on or about the great plateau of central Asia (Matthew 1950, 41) and rejected the ideas that the present habitat of primitive races was taken to be approximately the primeval home of man (Matthew 1950, 42). He saw the assumption that man is primarily adapted to a tropical climate as only partly true (Matthew 1950, 42). For

[238] The role of natural rafts like ice-floes and driftwood in the dispersal of plants and animals was already discussed by Darwin (1859, chapter 11) and Wallace (1876, e.g., vol. I, 14-15, 333, 402, 407, 416, vol. II, 35, 545, 548, 549).

[239] However, there are evident differences between his views and the ideas defended by Arldt. While Arldt's work *Die Entwicklung...* (Arldt 1907a) can be regarded as a culmination in the development of the land-bridge theories, Matthew was a persuasive opponent of these ideas.

this reason, and contrary to most authors before and after him, he did not consider it rational that the loss of body hair in the human species was a logical process for a primeval living in a warm climate. He regarded it as possible that the body hair reduced as a result of wearing clothes (Matthew 1950, 42-43). Similar vestiary hypotheses were later defended sporadically by modern authors (see, e.g., Kushlan 1985). Some years later, Matthew envisioned a scenario of a primeval horse deprived of its original forest environment and forced to adapt to open plains in his work *Evolution of the Horse* (Matthew 1913). As curator of fossil vertebrates at the American Museum, he had access to the world's largest collection of fossil horses. In the preface of one popular guide he wrote about this collection, and he confessed that "Among all the animals of past and present there is none so deserving of our interest and affection as the horse" (Matthew 1913, 7). In the same leaflet he speculated about the factors he believed were crucial for the emergence of the first horses:

> The evolution of the horse, adapting it to live on the dry plains, probably went hand in hand with the evolution of the plains themselves. [...] The coming of a cold, dry climate restricted and thinned the forests and caused the appearance and extension of open, grassy plains. The ancient forests inhabitants were forced either to retreat and disappear with the forests, or to adapt themselves to the new conditions of life. (Matthew 1913, 31; see also Matthew 1926, 171)

Matthew did not regard this scenario as a hypothesis. For him the fossil evidence showing a four-toed habitant of forests developing into a one-toed habitant of open plains was self-evident, so the whole scenario could not be regarded as a "theory", but as "a fact of record" (Matthew 1926, 176); see also chapter D.3.2, in which the argument is developed that the scenario of primeval man adapting to open plains was also regarded as a fact and not as a hypothesis.

A further interesting horse-man analogy was expressed by Matthew's early teacher Henry Fairfield Osborn (1857-1935), the influential American geologist, palaeontologist and director of the American Museum of Natural History in New York (Rainger 1991). Osborn believed in a very long and independent evolution of human beings, and he excluded an "ape-man" as a human ancestor. The similarities between apes and man, according to Osborn, are due to either a very remote common inheritance or to the convergent evolution of the ape towards the human type (see also Bender 1999a, 45-48; Bender-Oser 2004a, 64-71; Osborn 1927, 377).

Osborn was the most acclaimed proponent of the idea that central Asia was the birthplace of humans. As Matthew had done, he explained that the ideal environment of the ancestor of man was not in the warm forested lowlands "but in the relatively high, invigorating uplands of a country such as central Asia" (Osborn 1929, 6). He defended ideas on primeval man's evolution determined by climatic and environmental changes, presenting crucial events of his phylogeny in an oversimplified scenario. For instance, he stressed the idea of woodland and forest as places of stagnation (enough food, congenial life) and open plains as places of progression (less food, harsh conditions), both for the emergence of the primeval man and for the development of early civilisations (Osborn 1926b; 1927; 1928). He was convinced that "the home of primitive man should be looked for in the same kind of country in which the primitive horse flourished" (Osborn 1927, 337). This conviction was not based on convergent features between horses and humans, but was implicitly related to the idea that both organisms are "more developed" than other mammals. Osborn's conviction of the heuristic value of his horse-man analogy even motivated him to make predictions about the discovery of fossil remains of primeval man:

> It was my observation of the full-bred horse of Middle Pliocene time, known as *Pliohippus leidyanus*, which led me to predict to the National Academy of Sciences the discovery of a full-brained pro-man in Pliocene time; this prediction preceded the recent demonstration that *Eoanthropus dawsoni* of Piltdown is probably of Pliocene age. (Osborn 1927, 379)

Osborn was never confronted with the embarrassing fact that his prediction was not confirmed by any real empirical evidence - Piltdown was exposed as a hoax in the 1950s, many years after Osborn's death. Osborn's belief of the existence of the Dawn-Man in Asia was only a hypothesis, and one of the aims of the five expeditions to central Asia (1922-1930) led by Roy Chapman Andrews was to find hard evidence to corroborate Osborn's views (Andrews 1926). However, although these expeditions made important discoveries (Gallenkamp 2001) no fossil evidence for the Dawn-Man could be uncovered. Nevertheless, Andrews did not hesitate to present data on climates, temperature, botanic and general conditions in Pleistocene in clear support of Osborn's views (Andrews 1926, 248).

Although the contextualisation of early hominins in open plains had a long tradition in palaeoanthropology, a group of hypotheses often ignored the SHs by advocating that humans are essentially unspecialised and primitive creatures. Although these hypotheses were always considered as a poor alternative to the main hypotheses on human evolution, several influential authors belong to their advocates, and some important aspects of modern

hypotheses on hominoid/hominin evolution are influenced by these ideas. This is the topic for the next section.

D.6.2 Humans as primitive, unspecialized, deficient, cosmopolitan, "specialised in being unspecialised", auto-domesticated creatures

The present chapter has dealt with different hypotheses on human evolution which share some common elements or which were often discussed in the same theoretical framework. It begins with a summary of the primitivity ideas proposed by the German pathologist Maximilian Joseph Johann Westenhöfer, short Max Westenhöfer (1871-1957), as he is the author of another hypothesis on human evolution (the *Aquatile Hypothese*, see Appendix F) which is of crucial importance for a discussion on water use in early hominin evolution.

Westenhöfer is today a rather unknown pathologist (see Appendix F) who dedicated many years to anthropological research. Beside his professional activity as pathologist, he defended controversial views on human evolution which were published mainly in German medical periodicals, and in zoological journals;[240] he summarised his anthropological ideas in different books published between 1934 and 1948, with translations in Spanish and French.[241]

By means of several anatomical investigations Westenhöfer tried to demonstrate that primates and human beings developed in separate lines, and that a certain mammal or "amphibian reptile" was already "human" in a very remote time. In the title page of his book *Das Problem der Menschwerdung* he depicted an upright frill-necked lizard (*Chlamydosaurus kingii*) to illustrate his idea that the first mammals had already occasionally adopted an upright posture

[240] Westenhöfer published in periodicals specialised in different medical fields, as for instance urology, gynaecology (*Frauenkunde*), obstetrics, as well as in several clinical journals; some articles were published in zoological journals. Several of his articles were translated in Spanish and published in South American periodicals. A bibliography of Westenhöfer's publications on human evolution is given in (Westenhöfer 1942b, 390-391) as well as in (Bender-Oser 2004a, 154-156) and (Wicke 1958a).

[241] The first is a booklet with 71 pages entitled *Das Problem der Menschwerdung*. A second extended (106 pages) and revised edition with the same title was published in the next year (1935). A 52-page condensed and annotated French translation of this work was published under the title of *Le problem de la genèse de l'Homme*; the zoologist Serge Frechkop was responsible for this edition(Westenhöfer 1953). Westenhöfer largely extended *Das Problem* in the following years, but had problems in trying to publish it in Germany; also its translation in Italian and French were not approved "by the ruling powers in Germany at that time" (*damalige Machthabern in Deutschland*) (Westenhöfer 1948, 9). Therefore, according to Westenhöfer, the still unpublished book was translated by his former student Hector Rodriguez in Spanish and published in 1940 under the title of *El camino propio evolutivo y el origin del Hombre* (see Westenhöfer 1942a, 3); a further translation by the Chilean physician Edgardo Schirmer Ramos was later published (Westenhöfer 1951). The German edition of this work was later published under the title of *Der Eigenweg des Menschen*, which had two almost identical prints – only the subtitle diverged slightly - of 396 pages (Westenhöfer 1942a; Westenhöfer 1942b). In 1948, Westenhöfer published a 255-page extract of this book entitled *Die Grundlagen meiner Theorie vom Eigenweg des Menschen* (Westenhöfer 1948); see Bender-Oser (2004a)

when they evolved from an amphibian reptile [*Lurchreptil*] (Westenhöfer 1935, 75) (see Figure D.1).

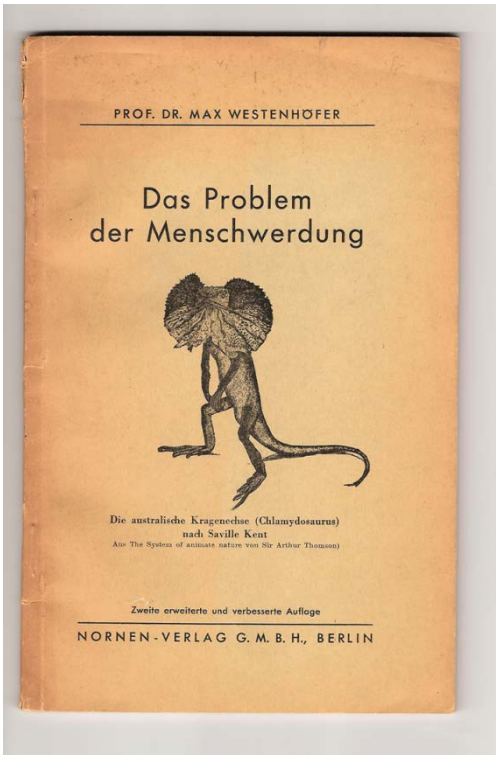

Figure D.1: Upright frill-necked lizard (*Chlamydosaurus kingii*) depicted in the title page of Westenhöfer's book *Das Problem der Menschwerdung.* This figure illustrates Westenhöfer's conviction that the first mammals were already occasional bipeds. He was certainly criticised for this picture, so that in the second edition of the book he emphasised that this illustration was only an example of upright posture of a living animal (Westenhöfer 1935, 3).

Westenhöfer, like other early authors[242], took pleasure in radically inverting the implied sequence of evolutionary events which led to the origin of humans. "We saw", wrote Westenhöfer, "that it is impossible that humans descended from an ape-like ancestor. The opposite is more likely" [*Das Umgekehrte ist wahrscheinlicher*][243] (Westenhöfer 1924, 256). Most proponents of what may be called "primitivity hypothesis" implied a naïve view of Dollo's law of irreversibility. The Dollo's law states that complex characters, once lost, are not regained. The naïve interpretation of this principle assumed that the reversal of simple

[242] For instance, the Argentinian zoologist Forentino Ameghino wrote: "Ce n'est pas l'Homme qui apparaît comme un Singe perfectionné, sinon au contraire les Singes qui apparaissent comme des hommes bestialisés" (Man is not an improved ape; on the contrary the apes are men that turned beastly) (Ameghino 1906), English translation by Podgorny (2005, 2).

[243] This radical inversion of the usual view of human evolution was often used by other early authors. In some few cases, similar statements were formulated by scientists after the modern synthesis, as for instance Björn Kurtén, who wrote: "Man did not descend from the apes. It would be more correct to say that apes and monkeys descended from early ancestors of man. The distinction is real: in the traits under consideration, man is primitive, apes and monkeys are specialized" (Kurtén 1973, vii).

features is also not possible. For instance, it was often argued that humans could not descend from a specialized ape bearing powerful teeth and long arms. Therefore, it was argued, the relative small canines[244] and short arms of humans were preserved in a lineage independent of other primates. This idea is suggested in the titles of some of Westenhöfer's works (my translation): "Man, the Oldest Mammal" (Westenhöfer 1926), "On the Primitive Place of Man Among the Mammals" (Westenhöfer 1930) or "Man's Own Way" (Westenhöfer 1942b). Instead of analysing Westenhöfer's specific arguments towards an "own road" in human phylogeny - for non-German speaking researches there are three available sources on these views published in different languages[245] - this study will proceed here to supply an outline of the historical context of this idea, which is important for an understanding of Westenhöfer's *Aquatile Hypothese* (see Appendix F).

Speculations about "apes descending from humans", ancestors of humans having already humanoid features in a very remote past or different human races developing from different ancient primate species were rather popular in the past. Different versions of these ideas were defended for instance by Karl Snell (1887), Albert Gaudry (1896), Hermann Klaatsch (1902; 1922), Carl Heinrich Stratz (1904), Julius Kollmann (1905), Florentino Amegnino (1906), Robert Wiedersheim (1908, 107, 126), Giuseppe Sergi (1913), Ludwig Wilser (1910), Maurus Horst (1913), Siegfried Knauer (1916), Henry F. Osborn (1926a; 1926b; 1927; 1928; 1929), Charles Hill-Tout (1921), Louis Bolk (1926), Otto Kleinschmidt (1926), Adolf Heilborn (1931), Paul Adloff (1907), Vincenzo Giuffrida-Ruggeri (1902; 1921), Francis G. Crookshank (1924), Edgar Dacqué (1924), Frederic Wood Jones (1918; 1948; 1929), Adolf Naef (1926a; 1926b; 1933), Heinrich Quiring (1930), F. Šamberger (1933a; 1933b), Klaas de Snoo (1942), Herbert Frietsche (1947), Friedrich A. Kipp (1948), W. C. Osman Hill (1950), Karl Beurlen (1950), Björn Kurtén (1973), to name but a few. This popularity is, at the first sight, not comprehensible, since an "independent" origin of humans was evidently incompatible with elementary facts. The influential German zoologist Adolf Remane criticised the aphoristic character and lack of basic knowledge on phylogenetic methods in Westenhöfer's primitivity arguments (Remane 1926). "Unfortunately", wrote Remane about

[244] Among German-speaking authors, the discussion on the canine-problem (*Eckzahnproblem*) was carried out especially by Paul Adloff, a proponent of primitivity ideas, and Adolf Remane, who defended the traditional views; see Remane (1928b) and references therein.

[245] For a review in English of Westenhöfer's ideas see Frechkop (1954), also a proponent of primitivity ideas; for a condensed French edition of Westenhöfer book *Das Problem der Menschwerdung* see (Westenhöfer 1953); for a summary of Westenhöfer's anthropological ideas in Spanish see Barrientos (1958) and specially the excellent papers by Hugo K. Sievers Wicke (Wicke 1958a; Wicke 1958b). For a lengthy analysis of Westenhöfer's anthropological ideas and a biography (in German) see Bender-Oser (2004a).

one of Westenhöfer's papers, "the work shows that the fantastic period in the phylogenetic research is not yet over" (Remane 1926, 235, my translation; see also Remane 1928a). Just as devastating (but expressed in a less abrasive tone) was a detailed review written by the Austrian zoologist J. Versluys (1929) (see Bender-Oser 2004a, 48-51). In his "Russian Manuscript",[246] Konrad Lorenz vehemently criticised the common method of formulating a hypothesis and afterwards finding examples to corroborate it, mentioning the primitivity ideas expressed by Westenhöfer and Edgar Dacqué (Lorenz 1992, 78). Bernhard Rensch also criticised Osborn's and Westenhöfer's primitivity hypotheses, naming them "naive ideas" (*naïve Vorstellungen*) (Rensch 1947, 310).

There are several reasons for the popularity of the primitivity hypotheses, most of them relate to the fact that the majority of the advocates of a primitivity hypotheses were ardent anti-Darwinians (or at least sceptical about the role of natural selection in evolutionary process) and defended essentialist conceptions in the sense of Platonic idealism. As the name suggests, essentialists working in biological fields believed that organisms have a permanent and unalterable "essence". Essentialists often draw obscure analogies between this "essence" and genetic material, pointing to heterochronic concepts to explain human 'unspecialised' anatomy. This was opportune at this time as genetics and evolution were regarded as mutually exclusive concepts and heterochronic concepts were often used as an alternative to natural selection (see below). The primitivity ideas were attractive to scholars who were interested in a discussion of 'human nature' in the tradition of ancient philosophers, i.e., without the restrictions of empirical corroboration required in evolutionary biology. In German speaking countries, authors who felt excluded from the discussion on the "unique status of man in nature" since the early 19th century and especially after 1859, found a niche in the so-called *Philosophische Anthropologie*, which consolidated to an own discipline in the 1920s through the works of Max Scheler (1874-1928), Helmuth Plessner (1892-1985) and Arnold Gehlen (1904-1976) (see Rehberg 2008). (Gehlen's ideas will be discussed below.)

Furthermore, the primitivity hypotheses were attractive to religious scholars and layperson searching for alternative ideas to the views defending a close relationship between humans and other primates. By assuming a very ancient human stem developing almost independently from other primates, proponents of the primitivity hypotheses created a comfortable distance between our own species and other organisms. From among the above list of authors

[246] This manuscript was written in Soviet prison camps between 1944 and 1948 and published for the first time in 1992.

defending primitivity ideas there can be found several scientists with a strong reputation in their own field in natural sciences, but who defended highly obscure and mystic ideas on human evolution in their attempt to conciliate evolutionary thinking with their religious beliefs. For instance, the metaphysical ideas on human evolution expressed by the German palaeontologist Edgar Dacqué (1878-1945) have more in common with the speculative ideas presented by the natural philosopher Lorenz Oken (see Appendix A, chapter A.4) than with the scientific ideas of early 20th century. It is, therefore, not surprising that Snell, Kipp, Dacqué, Westenhöfer, Bolk and other proponents of primitivity were often positively quoted by "zoological anthroposophists" (Rapp 1987; Schad 1971; Tittmann 1982; Verhulst 1999). Pseudo-scientific arguments claiming that humans exist since billions of years are today defended by creationists and theosophists.

Finally, another reason for the success of the primitivity hypotheses is related to two connected topics which were very influential in the anthropological discussion in late 19th and early 20th century. The first topic concerns the popular idea at this time that humans are unique concerning their alleged lack of specialisations when compared with other organisms. These views are derived from of the ancient philosophical ideas on "human nature", a topic which has been the subject of numerous studies on ancient ethnological and anthropological debate[247] and which will not be repeated here. The second topic concerns the view expressed by early and modern biologists which states that specialisation (or 'overspecialisation', as it is often termed) may lead to the extinction of species. This assumption is based on the seemingly comprehensible idea that organisms that are too committed to certain aspects of their environments will have more problems developing adaptive responses to changes in the environment than less specialised organisms. This idea motivated evolutionary biologists to supply stereotype explanations in which a causal link between the extinction of organisms and its alleged 'overspecialisation' was assumed. Through an inflexible interpretation of Dollo's law of irreversibility (see, e.g., Beurlen 1937, 21-48), early authors often identified which allegedly overspecialized organisms died out or which of the extant alleged overspecialised species would not be able to "develop further" (Schindewolf 1950, 327-328). Such predictions and reconstructions were often formulated in connection with orthogenetic ideas, coupled with criticism towards the influence of natural selection (Beurlen 1937, 66-73; Schindewolf 1950, 314-321, 410-417).

[247] See Müller (1997; 1968; 1980; 2003) and Landmann (1962). See also Stoczkowski (1994; 2002), who pointed to several similarities between modern and ancient theories.

It is therefore not surprising that several authors proposed ways by which living organisms may have prevented the danger of this biological sword of Damocles through heterochronic processes in the time prior to the consolidation of the modern syntheses – sometimes also afterwards. [248] Similarly, most proponents of primitivity hypotheses used the idea of man as a creature who "escaped" from the dangers extinction by "keeping specialised". The German geologist Heinrich Quiring (1885-1964), for instance, named an organism's ability to "escape" from the impasses related to specialisation a "negation" (*Negation*). He argued that in Tertiary times, man and monkey were part of the same clade (*Stamm*). During the climatic changes in the Ice Age, a part of these primates went to the south, following a more favourable region. Consequently, they adapted further to these conditions and their brain degenerated partially. The ancestor of man, however, stood in the cold climate and "negated" any adaptation. Quiring believed that a similar process of resistance against adaptation occurred in the evolution of other creatures, such as in the emergence of the first terrestrial vertebrates (1931; Quiring 1930); Barrell's and Lull's analogies between the emergence of humans and first terrestrial vertebrates have been mentioned in chapter D.6.1.

Similar ideas were proposed by other authors, such as Herman Klaatsch, who believed that humans did not evolve because of a struggle of life (*Kampf ums Dasein*), but because they were "spared" from the influence of natural selection (Klaatsch 1922, 47).[249] One of the most influential philosophical concepts in German-speaking countries relating to the advantages of the alleged lack of specialisation in humans was formulated by Arnold Gehlen. In his book *Der Mensch: Seine Natur und seine Stellung in der Welt* (first published in 1940) he discussed, among other issues, the views expressed by 18th and 19th century philosophers, contemporary scientists and proponents of primitivity hypotheses; he also knew Westenhöfer's works. Gehlen was especially interested in the anthropological ideas expressed by Johann Gottfried Herder (1744-1803), a very influential theologian and cultural philosopher in 18th century. Herder himself was inspired by contemporaneous and classical authors (Berg 1984; Gipper 1995; Häfner 1995; Lovejoy 1959b; Wenzel 1990). An excellent investigation of the *Mängelwesen*-idea by Gehlen, Herder and antique precursors is supplied by Pöhlmann (1970); see also Müller (1968). The idea of humans as anatomically inferior to other animals was also expressed by tribal people, as for instance in the poetry of South American indigenous Guaraní (in Theile 1962, 42). For an interesting discussion of the

[248] See for example the ideas expressed by Clark (1964, 247), Cloud (1948), Hardy (1954) and Hilzheimer (Clark 1964, 247; Cloud 1948; Hardy 1954; 1927).

[249] This is basically the same idea expressed by Herschel and Darwin (see chapter D.3.1). See also Gehlen (1986b, 128), who wrote about human ancestors living in a protected environment (a "paradise").

Mängelwesen-idea by an author in the 17th century see the book *De la perfection de l'homme* by Charles Sorel; this author was already mentioned elsewhere (Appendix B) in connection with de Maillet's ideas on aquatic counterparts to terrestrial animals. Sorel dedicated large parts of his work to defend the opinion of human as the most perfect organism and rejected therefore the ideas on human as inferior and deficient creatures (Sorel 1655). He discussed also theological implications of the plurality of worlds; his work was also translated into German (Sorel 1660).

Starting from the pre-conceived and untenable assumption that humans did not descend from any animal species (Gehlen 1986b, 14-15), he repeated views often expressed by classic philosophers which stated that humans, when compared with other organisms, are basically *Mängelwesen* ("deficient beings") and *weltoffen* (cosmopolitan). Gehlen (1986a, 14-16) borrowed the expression *Weltoffenheit* from the philosopher Max Scheller (1874-1928), who used it in his work *Die Stellung des Menschen im Kosmos,* (Scheller 2005), first published in 1928. The work is based on a talk entitled *Die Sonderstellung des Menschen* (the uniqueness of humankind) from 1927 – an expression very popular by advocates of primitivity ideas. The Swiss biologist and natural philosopher Adolf Portmann also used the expression (*Weltoffenheit des Menschen*) (human cosmopolitanism) with similar metaphysical arguments as Scheller and Gehlen. He regarded humans as radically divergent from all other environmentally-bound *(umweltgebunden*) creatures (Portmann 1969, 83) and believed that "human development is human" (*Unser gesamter Werdegang ist human*) (Portmann 1973, 64) – a similar statement to the idea of "humans descending from humans" often implicitly expressed by proponents of primitivity ideas. Portmann often used terms like *Geheimnis* (secret) or *Verborgenheit* (hiddenness) in connection with early phases in human evolution (Portmann 1973, 68). He regarded the topic human evolution is unsearchable by scientific means. Instead of searching for scientific answers to our origins, so Portmann said, we should acknowledge "the grandness of the secret reason" (*die Grösse des Geheimnisgrundes*) (Portmann 1969, 164), without explaining what exactly he meant by this statement.

One of the authors strongly influenced by Portmann was the biologist, anthropologist and Jesuit Paul Overhage (1906-1979) who wrote several works on human evolution using an impressive number of references (1959a; 1959b; 1959c; 1961; 1969). Exactly as Portmann had done, he continuously used phrases like human evolution is "still immersed in a heavy darkness of secrecy" (*schwere Dunkel des Geheimnisses*) (Overhage 1959a, 287). Overhage's and Portmann's views on human evolution were strongly influenced by the metaphysical

ideas expressed by the Jesuit Teilhard de Chardin (1956). According to Gehlen, early humans survived by keeping a generalist, primitivist and "deficient" status (Gehlen 1950).[250] Konrad Lorenz, when discussing Gehlen's ideas in 1954 (here quoted from a later edition, Lorenz 1967, 516-516), suggested replacing Gehlens' *Mängelwesen* through the similar paradoxical expression "spezialisiert auf Nicht-spezialisiert-sein" ("specialised in being unspecialised"), stressing with this term the human ability to produce a broad range of locomotory behaviours. Interestingly, some later authors used almost identical words, without quoting Lorenz's work, e.g., Haldane (1956) and Niemitz (2002). Consequently, several authors after Haldane believe that he was the first author of these ideas; see, e.g., Schmidbauer (1974) and Laughlin (1968). Views on humans able to carry out a broad spectrum of locomotory behaviours were already proposed by pre-Darwinian authors. For instance, the French author Jacques-Henri Bernardin de Saint-Pierre (1737-1814) in his book *Études de la nature* (here quoted from the translated edition *Studies of Nature*) stressed the human ability to swim and to dive (p. 53), and concluded anthropocentrically: "There is no animal whose body is susceptible of so many different movements; and I am tempted to believe, that he unites in himself all the possible varieties of animal motion, on seeing how he bends, kneels, creeps, slides, swims, tumbles himself into the form of an arch, rounds himself like a wheel, like a bowl, walks, runs, leaps, springs, mounts, descends, climbs; in a word, how his frame is equally adapted to clamber to the summit of the rock, and to walk on the surface of the snow; to traverse the river and the forest, to pick the moss of the fountain, and the fruit of the palm-tree; to feed the bee, and to tame the elephant" (De Saint Pierre 1799, 54-55). The alleged human uniqueness concerning locomotory ability is discussed in chapter 6 of the main thesis.

Additionally, Lorenz (1940; 1959) speculated about the possibility that several human features are the result of a process of "self-domestication". Basically, this idea suggests that humans had undergone anatomical or behavioural changes by relaxing forces of natural selection, in a process similar to domesticated animals. Similar analogies were formulated by early authors, such as Johann Friedrich Blumenbach (1806, 43), Eugen Fischer (1914), Max Hilzheimer (1927) and Hans Nachtsheim (1940); the same idea is also implied in Gehlen's *Mängelwesen*-hypothesis and Bolk's ideas on human neoteny (Bolk 1926) - to name a few

[250] Gehlen's arguments cannot be regarded as product of a scientific discussion and resemble the early natural theological discussions. For instance, the same basic idea of human as "deficient creatures" when compared with other animals was formulated in a religious work written by the Austrian theologian and prolific author of pedagogic books Jakob Glatz (1776-1831). He discussed the paradoxical situation of man made in the image and likeness of God but at the same time being, among all living creatures, the most susceptible to physical and psychic problems (Glatz 1814, 14-16).

examples. Several other authors pointed out the problems related to these ideas, such as specialists in domesticated animals (Herre 1959) and authors who criticised oversimplified assumptions on humans as essentially neotenic organisms (Starck 1962). Different versions of the self-domestication-hypotheses are still sporadically propagated by modern authors; see review and further references in (Brüne 2007).

As shown above, Herschel and Darwin speculated about the possibility that primeval man emerged on an island, protected from the selective pressure of big predators. In the early 20th century, different versions of the Herschel/Darwin island hypothesis were published. These authors often pointed to Australia or to a hypothetical sunken continent as cradle of mankind. Furthermore, they often related to a bodily inferiority and primitive/generalised status of humans when compared to other animals to corroborate these ideas. One of the most elaborate hypothesis of this type was proposed by the German anthropologist Otto Schoetensack (1850-1912) in a paper entitled *Die Bedeutung Australiens für die Herausbildung des Menschen aus seiner niederen Form* (1901). Schoetensack agreed with Hermann Klaatsch's[251] view which states that humans are unspecialised creatures, which separated from other primates in a far-distant time, even before the specialised arboreal features of apes developed. Schoetensack believed that human bipedalism and naked skin would represent a severe disadvantage in a dangerous environment. For this reason, these features did not evolve through a "struggle for survival", but quite the opposite, they could only develop if primeval man lived in a safe environment, rather protected from dangerous carnivores. For him, the most favourable place would be Australia; a point he shared with Klaatsch. On this continent a primeval man (who was already more intelligent than other creatures) would not have difficulties in hunting slow and clumsy [*langsam und plump*] marsupials. Like several palaeoanthropologists after him, he tried to envisage the exact environmental conditions crucial in primeval man. According to him, the human ancestor would never develop into humans in a forest habitat – rather it had to be a mix of forest and vast steppe in Australia that saved primeval man from unilateral specialisations typical for today's living apes (Schoetensack 1901, 131). Schoetensack's ideas did not remain unnoticed. Some years later, Enrique Müller de la Fuente (1906, 92-98) quoted Schoetensack and repeated his arguments of Australia as a place safe from big predators and

[251] The probably most famous proponent of primitivity ideas in German speaking countries, Klaatsch did not believe that humans descend from apes. He hypothesised that human bipedalism developed in connection with climbing high and isolated trees of a certain circumference. According to his view, bipedalism evolved long before the strong arboreal specialisations of other primates. Primeval man branched up from the main primate stock in a sunken continent in the Indian Ocean, close to Australia. The aborigines are isolated remnants of these primeval humans (Klaatsch 1922, 91-92).

for the development of bipedalism/hunting in a landscape characterised by less vegetation and more open plains (Müller de la Fuente 1906, 94-96).

Schoetensack's hypothesis is also interesting for another reason. Darwin did not recognise or justify the evident contradiction between his open plains ideas and his island hypothesis. Although we cannot say if Schoetensack was indirectly or directly influenced by Darwin, or if the German author came to a similar set of ideas independently, his scenario is remarkable in the sense that it not only combines the island with the open plains hypothesis, but even merges both models with the idea of humans as helpless and primitive creatures.

It would be wrong to assume that the primitivity hypotheses, being too divergent from the common view on human evolution, did not have a relevant influence on latter palaeoanthropological hypotheses. Similar views of proto-hominins as not "too specialised" are implied in in several influential hypotheses on the emergence of bipedalism, as for instance in the "quadrupedal hypotheses", [252] which were popular until the 1960s (Abel 1931, 135; Clark 1940, 207; Heberer 1951a, 52; Heberer 1973, 32-34; Schwalbe 1923, 323; Straus 1949; Straus 1940) (Le Gros Clark later changed his ideas (Clark 1946)). This model posits that the hominin ancestor was not arboreal, but a terrestrial and palmigrade or digitigrade quadruped on open plains or mosaic landscapes. Their proponents excluded the existence of suspensory (and consequently knuckle-walking) adaptations among proto-hominins, as they assumed (similar to the advocates of the primitivity hypotheses) that such specialisations are not compatible with the prerequisites of a hominin ancestor. They assumed that a quadrupedal proto-hominin would better fulfill the prerequisites of a "generalist proto-hominin" than a brachiatory proto-hominin.

Adolf Remane, who was already one of the sharpest critics of the primitivity hypotheses, also criticized the early quadrupedal model. He, among others, argued that attempts to see a terrestrial quadruped *Proconsul*[253] or the earlier terrestrial primate as human ancestors (which

[252] Sarmiento proposed later a modified form of the quadrupedal hypotheses, in which he defended a similar idea, with some additional and intricate steps based on an analysis of terrestrial traits of gorillas (Sarmiento 1994) and contextualising early hominin evolution in open plains (Sarmiento 1998).

[253] *Dryopithecus* and *Proconsul* were often regarded as ancestors or closely related to ancestors of humans; see for instance Heberer (1951b, 6, 17) who regarded both groups as possible human ancestors. The idea of *Proconsul* as a human ancestor is also implied in several illustrations in biological textbooks, sometimes in educational tables; see for instance an educational table entitled "*Horde der Prokonsulaffen*" (horde of proconsul monkeys), depicting several terrestrial (some quadrupedal, some upright) and climbing animals searching for food in a savannah environment. It was published by the *Akademie der pädagogischen Wissenschaften der DDR,* a research institute active from 1970 to 1991, created with the specific purpose of promoting knowledge compatible with Marxist-Leninist views in the GDR (Malycha 2008).

automatically excluded a common ancestor between humans and apes) was highly improbable. He showed that the structural specialisation of an organ for a certain activity is not accompanied by a depletion of secondary functions, but may directly lead to the development of new secondary functions (Remane 1956); see also Avis (1962). In fact, a comparison between Remane's criticism of Westenhöfer's primitivity ideas (quoted above) and his criticism of the authors who denied an arboreal phase in hominin phylogeny shows that the arguments are basically the same. Certainly, the primitivity hypotheses were motivated by orthogenetic, essentialistic and anti-Darwinian views – aspects which were not characteristic of most quadrupedal hypotheses – and in Germany, anti-Darwinian and non-Darwinian concepts were criticised not only through scientific arguments, but also for ideological reasons.[254] However, the problems related to the corroboration of the primitivity hypotheses and the quadrupedal hypotheses are basically the same, since both assume a non-parsimonious exclusion of arboreal specialisations from hominoid/hominin phylogeny.

The quadrupedal hypotheses lost much of their popularity (but see[255]), on one hand because molecular findings of the 1960s suggested a much more recent date for the ape-hominin-split (Sarich & Wilson 1967), on the other hand because an arboreal proto-hominin was never incompatible with the development of hominin bipedalism (Franzen 1972; Franzen 1997; Remane 1956). Finally, increasing fossil evidence showed clear arboreal adaptations in early hominins (Berger & Tobias 1996). One of the most important discussions in the last decades concerning the evolution of bipedalism in early hominins concerned knuckle-walking, a topic revised by (Richmond et al. 2001, and references therein) and discussed in chapter 6 in the main thesis.

D.6.3 The aquatic hypothesis: origin, reception and further development

Most arguments of what today is usually called the "Aquatic Ape Theory" or "Aquatic Ape Hypothesis" – here we prefer the term "aquatic hypothesis" (AH), was first formulated by the German pathologist Max Westenhöfer in 1923 (see Appendix F). However, as almost the entire discussion on this topic was carried out in connection with the ideas proposed by the Alister Hardy and Elaine Morgan, the present chapter focuses on these authors.

[254] For instance, the influential German anthropologist Gerhard Heberer (1901-1973) and proponent of a quadrupedal hypothesis was a member of the NSDAP (*Nationalsozialistische Deutsche Arbeiterpartei*) and SS. He criticised Westenhöfer's anti-Darwinian ideas as being not compatible with Nazi ideology, calling him one of the *Dunkelmänner* (man of the darkness) (see Bender-Oser 2004a, 45-47 and references therein).

[255] Carsten Niemitz's statement "it is the most parsimonious derivation to propose that our non-human primate ancestors never came down from the trees: They merely stayed where they were anyway – e.g., "on the ground" can be considered as one of the rare modern proponents of the old quadrupedal hypotheses (Niemitz 2010, 26).

Hardy's aquatic hypothesis

On 5 March 1960 the British marine biologist Alister Hardy (1896-1985) was asked to address a conference of the British SubAqua Club at Brighton. There he proposed basically the same ideas as defended by Westenhöfer. Since his aquatic hypothesis appeared abbreviated in the daily press,[256] he accepted the invitation of *The New Scientist* to give a fuller statement of his aquatic hypothesis (AH) (Hardy 1960b, 642). In a paper entitled "*Was man more aquatic in the past?"* he stated that he was toying with the concept of man's evolution in a semi-aquatic environment for many years; he hesitated to present this idea because it had seemed too fantastic to him (Hardy 1960b, 642). However, the more he reflected upon it, the more he "came to believe it to be possible, or even likely" (Hardy 1960b, 642). He supplied a short outline of the evolution of vertebrates from aquatic to terrestrial animals "only because it forms the background to another story, one that is not quite so familiar to those who are not trained as zoologists" (Hardy 1960b, 642): several terrestrial vertebrates from different groups went "back" into the water to make a living, "because there was not enough food for them on the land" (Hardy 1960b, 642). As examples he mentioned among the reptiles the ichthyosaurs, the plesiosaurs, many marine crocodile-like animals, turtles, and water-snakes; among the extant mammals he mentioned the cetaceans, the dugongs and manatees, the semi-aquatic seals, polar bears, otters, various aquatic rodents (like the water voles and the coypu), insectivores (like the water shrew) and the platypus; among the birds the penguins are the supreme examples (Hardy 1960b, 642).

Hardy admitted that the suggestion he was about to make may at first seemed far-fetched, yet he thought that it may best explain the striking physical differences that separate man's immediate ancestors from the more ape-like forms. He suggested that a common ancestor of both groups "was forced by competition from life in the trees to feed on the sea-shores and to hunt for food, shell fish, sea-urchins, etc., in the shallow waters off the coast". He had rather clear ideas about the environmental contextualization of this semi-aquatic phase:

> I suppose that they were forced into the water just as we have seen happen in so many other groups of terrestrial animals. I am imagining this happening in the warmer parts of the world, in the tropical seas where Man could stand being in the water for relatively long periods, that is, several hours at a stretch. I imagine him wading, at first perhaps still crouching, almost on all fours, groping about in the water, digging for shell fish, but becoming gradually more adept at swimming. Then, in time, I see him becoming more and more of an aquatic animal going

[256] According to (Sanderson 1961, 141), it appeared in *New York Herald Tribune*, of March 7, 1960.

> farther out from the shore; I see him diving for shell fish, prising out worms, burrowing crabs and bivalves from the sands at the bottom of shallow seas, and breaking open sea-urchins, and then, with increasing skill, capturing fish with his hands. (Hardy 1960b, 642-643)

Hardy pointed to some alleged anatomical, physiological and behavioural similarities between humans and aquatic mammals, suggesting that reduced body hair, a layer of subcutaneous fat, erect posture and underwater swimming abilities evolved when early hominins exploited food resources in lakes, rivers or coastal environments.

The AH was not the first scenario which criticized the open plains ideas. For instance, the Austrian palaeontologist and palaeobiologist Othenio Abel (1875-1946) regarded the open plains idea as not specially insightful; he proposed that between the arboreal phase and the terrestrial phase primeval man lived as a creature adapted to climbing in a mountainous region (Abel 1931, 379). Other authors defended the idea that climatic and environmental changes did not play a crucial role as driving factors in hominin evolution. Instead, first primeval man descended from the trees because they were allegedly too heavy to stay on them (Beurlen 1950; Rensch 1972, 325; Weidenreich 1939). However, the AH introduced a new component in the way that scientists perceived the SHs. For the first time in palaeoanthropological discourse, classical ideas were challenged by a scenario which implied hominins interacting intensively with water, a view which was often perceived as diametrically opposed to the open plains ideas. Hardy never wrote a book on the AH; he published some other articles on this topic (Hardy 1960a; Hardy 1960c; Hardy 1977).

The first reaction to the AH began soon after Hardy's publication of his paper (on letters published in *The New Scientist* in 1960 see Appendix F). It was no one less than Raymond Dart who addressed a criticism to this new scenario in the same magazine. As the title of his almost unknown paper suggests, *The recency of man's aquatic past*, Dart also considered human relation to water as significant. However, in opposition to Hardy, he regarded it not as product of an early hominin semi-aquatic phase, but rather as a recent innovation in human evolution, "far more drastic and significant" than Hardy suggested (Dart 1960, 1669). Dart wrote:

> Man's interest in water creatures, therefore, goes a moderate way back, but scarcely as far as Sir Alister proposes. Taungs and Makapansgat have shown us that the South African man-apes, the australopithecines, extracted crabs and turtles out of streams. Even when men's brains were no bigger than those of gorillas they recognized food in brooks as well as on dry land. But they could not catch fish. So Mr. William F. Fahy (in his letter which *The New*

> *Scientist* published on April 7 [1960]) was right in saying that it is not necessary to postulate an aquatic habitat to explain Man's origin from apehood. There is no evidence that Man's hairlessness, his erectness or his earliest use of tools were gifts from a type of water-living ape. (Dart 1960, 1669)

Dart's statement can be considered as the beginning of a long tradition among palaeoanthropologists to misinterpret Hardy's ideas, presenting early hominins as much more aquatic as actually exposed in Hardy's scenario. For instance, a hominin with the ability to catch fast swimming fishes with the hands would certainly imply a high level of aquatic adaptation, comparable with high specializations of dolphins, seals or otters. Since this is obviously unlikely, Dart's comment on hominin inability to "catch fish" exposed the whole aquatic scenario as implausible. However, Dart did not quote precisely Hardy's ideas. What Hardy actually meant was following: "My thesis is that a branch of this primitive ape-stock was forced by competition from life in the trees to feed on the sea-shores and to hunt for food, shell fish, sea-urchins, etc., in the shallow waters of the coast" (Hardy 1960b, 642), and only after increasing skill, early hominins would perhaps be able to capture fish with their hands " (Hardy 1960b, 643). In fact, Dart seemed to ignore that modern humans are able under certain conditions to catch fishes with the hands (see chapter 5.4.4 in the main thesis).

There are several similar misleading emphases of the degree of aquatic adaptation in early hominins. For instance, in Valkenburg (Netherlands), a conference, organized by the European Sociobiological Society and the Dutch Association of Physical Anthropology, was held in August 1987. The participants had the aim to evaluate the pros and cons of the AH. In the 24 contributions of the book resulting from the conference, 10 were pro AH, 9 contra, and 5 suggested a kind of a "less aquatic" or "mild" version of the AH. For instance, Matcheld Roede (one of the editors of the book) argued that the AH covers only the relatively brief Miocene period 5 to 3.5-4 million years ago, and therefore "there does not seen enough time for *complete water adaptation* to have evolved. The alleged aquatic ape can *only been semi-aquatic* – or, more probably, just coastally foraging" (Roede 1991, 287, italics added). Vernold Reynolds, another editor of the work, argued in a similar way, when he writes that "human ancestors were never *truly aquatic*" (Reynolds 1991, 331, italics added). Both authors follow with their statements a persistent element in the reception of the AH, exposing Hardy's evolutionary scenario as more aquatic than originally assumed. The aim of this caricatured view of the AH was manifold: it was sometimes used by authors fascinated by some arguments of the AH but afraid of being stigmatised as advocators of a radical idea, and at the

same time supplied a rational for the formulation of an alleged "mild version" of the AH (as probably in the case of Roede's and Reynold's statements), or to facilitate a falsification of the AH (see below), or in attempts to present a compromise between AH and SH (about compromises see below).

It is therefore not surprising that the aquatic hypothesis was immediately regarded as an extremely improbable scenario and as an example of bad science. Even the anthropologist Grover S. Krantz, famous through his books on the existence of Bigfoot, considered Hardy's AH as "so contradicted by the facts as not to be worthy of rebuttal here" (Krantz, 1992, 52).[257] Despite the fact that the AH was perceived as highly controversial, not all SHs' proponents were inclined to refuse it a priori. Some authors regarded it as possible to integrate the aquatic scenario in the SH's framework, instead of seeing it as an attempt to replace the open plains ideas. For instance, when the British zoologist and popular author Desmond Morris presented his own interpretation of the role of hunting on open plains in early hominin evolution in his best seller *The Naked Ape*, he provided a fair summary of Hardy's aquatic hypothesis, characterizing its indirect evidence "appealing" but without "solid support" (Morris 1967, 45). Inspired by Hardy's attempts to envision the aquatic ape as a predecessor of a hunting hominin adapted to open plains (Hardy 1960b), Morris decided to assume a neutral and conciliatory position: "Even if eventually it does turn out to be true, it will not clash seriously with the general picture of the hunting ape's evolution out of a ground ape. It will simply mean that the ground ape went through a rather salutary 'christening' ceremony!" (Morris 1967, 45).

In a footnote in his book, *The Biology of God*, Hardy agreed with Morris' conciliatory comments, but did not accept the hypothetical aquatic phase's secondary role squeezed between an arboreal ancestor and a savannah adapted hominin. Inspired by Morris' Christian metaphor, he argued: "[…] if [the AH is] true, I think it was rather more than a mere christening – it was the all-important weaning from the fruits of the trees to flesh by way of succulent bivalves and other tender 'fruits of the sea'" (Hardy 1975, 158).

Elaine Morgan's development of Hardy's Aquatic Hypothesis

The AH would probably have become a bizarre footnote in the history of palaeoanthropology without recognizable impact on the SHs' reception, if it had not become entangled with

[257] However, not all cryptozoologists were so sceptic about the AH, see Sanderson's statements in Appendix B, chapter B.2.

developments which initially took place outside of scientific debate. Until the middle 1960s, palaeoanthropological discussion was characterized by the idea that man had the active role in early hominin evolution, a concept historically connected to the dominant role of male hunters as seen in today's hunter-gatherer societies. As already shown in chapter D.4.3, although Dart and Ardrey did not initiate the discussion on the role of hunting in early hominin evolution, Ardrey's skills in depicting early humans as hunters in open plains and the popularity of his books contributed to instigate a fundamental discussion on the role of women in hominin evolution. On one hand, ethnological and palaeoanthropological publications increasingly stressed the female contribution to reproductive success through gathering and preparing food, mitigating the role of hunting in early hominin evolution (Tanner 1987; see Zihlman 1981). However, as these concepts stressed the role of females in food acquisition in savannah woodlands and grasslands, they did not challenge the general framework of the savannah paradigm.

A completely different development was initiated by the Welsh writer and journalist Elaine Morgan (1920-2013). She felt immediately attracted to the AH – when she read about it she felt "as if the whole evolutionary landscape had been transformed by a blinding flash of light" (Morgan 1972, 31).) Another factor which rendered this scenario attractive to her was the possibility to interpret human evolution without the androcentry implied in classical hunting hypotheses. Morgan's own evolutionary scenario mitigated the relevance of hunting technology and male hunters as main meat deliverers, since animal protein could also be provided by early hominin females and children when gathering shells in a coastal environment. In a book insightfully entitled *The Descent of Woman* (1972), Morgan pointed out several problems related to an incipient hominin adaptation to open plains, addressing specifically Ardrey's, Dart's and Morris' ideas (Morgan 1972, 11-17). In later publications Morgan reinforced her criticism of the SHs, using a more scientific approach and abandoning the feminist discourse (Morgan 1972, 11-17; 1982, 19-20; 1984). She named the open plains idea "savannah theory" (Morgan 1982, 19-20), a term used regularly in palaeoanthropological publications since the 1990s (Langdon 1997; Roede et al. 1991).

In her book *The Scars of Evolution* Morgan wrote ideas concerning water from the point of view of evolutionary medicine[258]. Although hydrotherapy as a long tradition in medicine, this

[258] As already stated elsewhere, to my knowledge, the first ideas on the importance of water for human health formulated in an evolutionary context were formulated by Benoît de Maillet. The perhaps first treatises discussing in details problems related to an upright posture is the booklet *Delle corporee differenze essenziali che passano fra la struttura de' bruti, e la umana* (Moscati 1771a) written by the Italian physician Pietro

topic was almost completely ignored in evolutionary medicine, mainly due to the lack of a theoretical framework in which this issue could be discussed.

Adverse attitude toward topics associating early hominin interaction with water

The AH never gained widespread acceptance, and was mostly rejected (Dart 1960; Gowlett 1984, 17; Langdon 1997; Pickford 1991; Wheeler 1991) or ignored in palaeoanthropological debate. However, it contributed significantly to how the savannah scenario was perceived in popular and scientific discourse on human evolution since the 1980s. In opposition to early publications, which treated the savannah idea as mere description of facts, the open plains scenario became increasingly perceived as a hypothetical construct, subjected to the normal process of scientific validation.

In a paper published in the *Journal of Human Evolution* the anthropologist John Langdon wrote one of the best criticisms towards some specific arguments of the AH. In this paper, he tried to define the SH: "The savannah theory is, in fact, the collective discipline of palaeoanthropology. It encompasses all the frequently proposed and rejected models, discussions, debates, and hypotheses that assume a terrestrial habitat for all stages of human evolution" (Langdon 1997, 490). This definition is peculiar, since theories and disciplines cannot be used to define each other: scientists working within a discipline formulate, defend and reject different hypotheses, and palaeoanthropology is not an exception to this process. Even if Langdon intended to explain the savannah theory as the *product* of the collective discipline of palaeoanthropology, this definition still does not hold with evident historical facts. Previously mentioned Othenio Abel's 'cliff hypothesis' (Abel 1931) was formulated as an alternative to the classical SHs. Another example is the influential model proposed by the Swiss primatologists Christophe and Hedwige Boesch, in which early hominin evolution is contextualized in a forest environment (Boesch & Boesch 1984a; Boesch & Boesch 1984b).

Moscati (1740-1824). After a comparison between the anatomy of man and "unreasoning animals" (animali bruti) he came to the conclusion that one of the most conspicuous divergencies is the upright posture. He recognized already the upright posture as the cause for several orthopaedic, cardiovascular, intestinal and gynaecological diseases. The German translation of this work (Moscati 1771b) was quoted by Gottfried Herder in his *Ideen zur Geschichte der Menschheit* (Herder 1853, vol. 28, 154). Moscati's pioneer work is notable. When hundred years later Darwin published his *Descent of Man*, he did not discuss the implication of his evolutionary ideas in human medicine. Today, the beginning of the modern evolutionary medicine is often related to works published from the 1950s on; see, e.g., Williams (1957). Evolutionary medicine is usually considered as irrelevant in most medical education programs (Nesse et al. 2006; Nesse & Williams 1995), but there are indications that this started to change (Nesse et al. 2010).

Langdon's definition implies a clear distinction between SHs as related to research carried out within "the collective discipline of palaeoanthropology" and AHs as models defended by amateurs, such as science writers working outside of palaeoanthropology. This distinction is for several reasons misleading. First, we saw the crucial role of science writer Robert Ardrey in the popularization of the SHs in the 1960s and the role of science writer Elaine Morgan in the process through which the savannah model was recognized as a hypothetical construct. Second, not all proponents of the aquatic model regarded it as completely incompatible with the classical views. We saw that Alister Hardy proposed his AH as a phase between forest and savannah. On the other hand, not all scientists working within palaeoanthropology or engaged in the popularization or development of classical palaeoanthropological ideas saw the SHs and AHs as completely incompatible models. We saw above that Hardy's narrative inspired Desmond Morris' attempt to squeeze the aquatic phase between an arboreal and savannah phase. Later, the Dutch evolutionary biologist Sarah B. M. Kraak undertook an attempt to fuse the AH and SH in a book chapter insightfully entitled *The answer: the Aquatic Ape Theory and the Savannah Theory combined* (see also Knight 1991, 235-244; Kraak 1991). Furthermore, AHs' critics give more attention to the ideas proposed by non-academics than to publications by specialists who recognize the need for a scientific study of early hominins' interaction with water (Crawford & Marsh 1989; Cunnane et al. 1993; Richards 1987, 193-204; Schagatay 1996; Tobias 2010; Wrangham 2005; Wrangham et al. 2009). Finally, little attention is given to palaeoanthropological scenarios for early hominin evolution that diverged considerable from the SHs exposed in textbooks by depicting early hominins exploiting coastal environment, wet savannah or marsh communities (Geist 1978, 215-218; Hewes 1972, 22-23).

As it is clear in the examples above, and although Langdon's criticism against some flawed arguments of the AH were correct, his *definition* of SHs is based on an artificial delimitation of what belongs to palaeoanthropological discipline. All these problems with the SH's definition can be circumvented by focusing on the common components of these ideas. Although there are several deviations among the different savannah scenarios concerning geographical and temporal frameworks, specific ecological settings and sequence of evolutionary events, all these hypotheses share the evident characteristics of early humans evolving several key features in the context of an open or semi-open environment (Bender 1999a, 35-80).

Langdon's SHs definition reflects an interesting dilemma in palaeoanthropology which is present to date. Based on palaeoclimatic and fossil data, several palaeoanthropologists in the 1990s[259] expressed doubts on the SHs. Although this evidence formerly confirmed Elaine Morgan's objections to this model, palaeoanthropologists had difficulties accepting Morgan's criticism of the SHs as useful contribution to palaeoanthropological discussion without promoting the AHs. This attitude is clearly recognizable in following statement by Langdon:

> The savannah hypothesis that Morgan criticizes turns out to be a straw man. Anyone who dredges up a century of hypotheses can find many to ridicule; but if the field has already rejected them, the exercise is pointless. In fact, scholars are now discarding the savannah setting for hominin divergence. (Langdon 1997, 490)

Langdon's straw-man statement stands in stark contrast to the following sentences by Roger Lewin and Robert A. Foley:

> Palaeoanthropology has a reputation for controversies and arguments, with major disagreements about who is who, and who is related to whom, among the fossil hominins. However, although there is considerable debate about the details, there is nonetheless remarkable consensus about the major aspects of human evolution – that our ancestors were derived from a population of African apes, adapting in increasingly open and savannah environments to the changing conditions. Most features, especially bipedalism, are seen as related to this change. (Lewin & Foley 2004, 282, our italics)

The contradiction between Langdon's and Lewin/Foley's statements reflects the divergence in their basic attitudes: Langdon attempted to exclude the AHs from palaeoanthropological discussion, while Lewin and Foley, as we will see later, mentioned the AHs when asking basic questions on the process of evaluation of alternative hypotheses in palaeoanthropology.

Lewin and Foley are correct in emphasizing the SHs' influence in modern palaeoanthropology. Although the SHs as a general model to contextualize early hominin evolution have been increasingly criticized in the last two decades, this model is still influential in different hypotheses using the same arguments and narrative expressed in classical savannah scenarios. For example, in the *Journal of Human Evolution* (the same

[259] This topic will be reviewed elsewhere. Briefly, criticisms of certain aspects of the SHs were punctually expressed by palaeoanthropologists in the 1980s and more emphatically from the 1990s onwards (see, e.g., Tobias 1995). Specialists today are more and more convinced that earliest bipedalism occurred in a forest context and a shift to more open country occurred two million years after the appearance of first bipedal hominins. In opposition to the classical SHs, to date there are no clear concepts about the factors influencing the emergence of bipedalism (see chapter 6 in the main thesis).

journal where Langdon published his paper), the zoologist Peter Wheeler published a series of papers between 1984 and 1996 defending his ideas on the thermoregulatory advantages of hominin bipedalism, naked skin and larger body size in the context of open plains or mosaic landscapes (see Wheeler 1994 and references therein). Wheeler's specific SHs belong to the most-quoted models on human bipedalism in contemporary palaeoanthropology. It is paradoxical that this remains true even after researchers are increasingly reaching consensus that the evolution of bipedalism cannot be contextualized in open plains (see chapter 6 in the main thesis).

An interesting example of the complexity of processes involved in the evaluation of ideas in palaeoanthropology is supplied by publications which positively mentioned Wheeler's hypotheses and at the same time deliberately pointed out that there is little evidence for a sudden shift from more forested to more grassland habitats during an early phase of hominin evolution (e.g., Conroy 2005, 51-54, 337-341)[260]. Additional evidence for the complex hypotheses evaluation is supplied by the specific views on early hominins defended by AHs' critics. For instance, Wheeler challenged the aquatic hypotheses on thermoregulatory grounds alone, emphasizing his own ideas on this topic (Wheeler 1991); see also Preuschoft and Preuschoft (1991), who similarly quoted Wheeler's view in their criticism towards the AHs. However, Langdon coined Wheeler's hypothesis as "entirely speculative", since this scenario "is also rooted in the assumption that a savannah environment had a key role in hominin origins", a concept that he regards as wrong (Langdon 2005, 125). This is only one of many examples demonstrating that defending palaeoanthropology from the intrusion of alternative ideas does not necessarily imply a consensus on classical views.

Coming back to the question formulated in the introduction of the present chapter: Which factors are influential in the process leading to consensus in palaeoanthropology? In their book *Principles of Human Evolution* (2004) Lewin and Foley touch this question by referring specifically to the savannah and aquatic hypotheses.[261] These statements deserve a full quotation, since this is one of few cases in which authors with impeccable reputations in palaeoanthropology refer to the AH to formulate fundamental questions on the evaluative

[260] It is fair to note that the same author (Conroy 2005, 337, footnote 12) also refers to views challenging Wheeler's ideas.

[261] Lewin and Foley wrote about the AHs in a "Beyond the Facts" section of their textbook, which was conceived as a didactic tool to stimulate students to think about how to assess alternative ideas in palaeoanthropology. As such, the quoted pieces reflect the state of the debate more than their own personal views on this topic (Foley, pers. comm.).

process of alternative ideas in this field: ”The issue: the idea that human evolution was triggered by an aquatic phase is widely supported and discussed outside the mainstream of palaeoanthropology, but is dismissed by most scientists working in the field. How do we determine what models are reasonable and plausible, and which ones are worthy of serious scientific study?” (Lewin & Foley 2004, 282). After an outline of the AH they continue: “Indeed, it is one of Elaine Morgan’s complaints that her ideas have been ignored rather than criticized or dismissed, and that this is a case of ‘normal science,’ in the terms of philosophers of science Thomas Kuhn, ignoring the radical alternative paradigm rather than engaging with it” (Lewin & Foley 2004, 283). After pointing out that the AH is “one among many ‘alternative theories’ of human origins, and indeed in that light is one of the most cogent and best argued” (Lewin & Foley 2004, 283), they continue:

> The existence of such models does raise the question of what it is that distinguishes a plausible model from an implausible one. What is it that makes it reasonable to discuss one model and to dismiss another out of hand? Is the aquatic ape hypothesis a reasonable explanation for many unique features of humanity, and ignored because it is a challenge to scientific orthodoxy, or is it a crackpot theory? If it is the latter, then should the scientific community spent time and resources refuting it? If it is the former, how can it become accepted as a good model? (Lewin & Foley 2004, 283)

It is impossible to give an objective answer to the above questions without an in-depth analysis of the role of water in early hominin evolution. Paradoxically, as long as topics related to hominin interaction with water are regarded as a domain of the AHs, palaeoanthropologists have little motivation to undertake such analyses. As a result of this stalemate situation, a serious imbalance can be detected in early and modern palaeoanthropological research: aspects of the reconstruction of human’s past directly related to well-established models proposed to contextualize early hominin evolution are much better studied than those topics which seem to contradict traditional models.

D.7 Conclusions

Few scientists will deny the importance of empirical evidence in palaeoanthropological research. Similarly, most palaeoanthropologists would probably agree that in recent decades this field has improved immensely, both the degree of interaction with other disciplines as well as its empirical basis. However, as promoted in this chapter, the use of empirical data and analogical reasoning in the formulation of hypotheses on hominin evolution is much more complex than often implied in palaeoanthropological publications. I have assumed here that

especially in scenarios proposed to contextualize early hominin evolution, serious misconceptions exist about what should be considered as sound scientific method or an educated scientific hypothesis, corroborated by strong empirical evidence, and what is a flawed method or a hypothesis lacking any empirical foundation. The recognition of these misconceptions is fundamental for progress in current palaeoanthropological research. Following are the summarised theses promoted in this chapter:

(a) Contrary to widespread opinion, the savannah hypotheses (SHs) were formulated long before empirical evidence was available. This fact has immediate relevance for modern palaeoanthropological discussion. First, several issues around alternative hypotheses on early hominin evolution (e.g., the factors responsible for the amazingly alternative hypotheses, and also how alternative hypotheses were formulated and criticized) were severely biased by reliance on what is believed to be a solid empirical corroboration of traditional scenarios. Second, theoretical positions strongly related to the SHs had a negative influence on how empirical evidence was gathered, analyzed and interpreted. I argue that one of the most important factors for improvements in palaeoanthropological research is the identification and exclusion of these biases, a process which requires a more serious participation of historians of science in the palaeoanthropological discussion than we have seen so far. Finally, the modification of the savannah scenario in recent years, sometimes regarded as a paradigm change in palaeoanthropological research, is basically a rearrangement and recycling of traditional SHs, and as such are exposed to similar criticism as the concepts that they poised to replace; this argument was developed in chapter 6 in the main thesis.

(b) A similar situation as described in (a) can be detected in the analogical reasoning used to formulate traditional hypotheses on early hominin evolution: in several cases, the use of referential models to contextualize early hominin evolution was not the starting point of new hypotheses, but was primarily relied on believing in traditional scenarios on human evolution. Based on the material analysed, I assume that these referential models are characterized by serious methodological flaws; this same problem applies to both traditional and alternative scenarios on early hominin evolution.

(c) Several historians of palaeoanthropology emphasize that the discussion on human evolution is characterized by multiple hypotheses. This is basically correct. It is well known that several aspects of hominin evolution – e.g., the precise sequence in the evolution of different hominin features or the hominin status of fossil primates – were controversially debated. However, we show this is not true concerning hypotheses presented as “scenarios” of early hominin evolution; these models are characterized by a strong tendency to rely on a single and in many sense oversimplified picture on hominin evolution, as presented in points (d), (e), (f) and (g).

(d) Until a few years ago, the strong focus on SHs prevented the formulation of concurrent hypotheses that challenged the traditional contextualization of early hominins in open plains. Instead of developing a healthy skepticism towards the old open plains-ideas, specialists adapted and integrated basic premises of the model into modern palaeoanthropological research. The subsequent scientific debate was carried

out mainly with the corroboration and falsification of versions of the savannah scenario – by discussing early hominin evolution in different spatial and temporal frameworks or by promoting different auxiliary hypotheses on the adaptive value of different hominin features. I propose that alternative hypotheses to the SHs are crucial, taking into consideration that the interpretation of early events is hominin evolution is still characterized by a high degree of uncertainty.

(e) Beside the factors explained in point (d), one crucial aspect for the broad acceptance of some of auxiliary SHs is the need to formulate new questions on early hominin evolution that can be answered with empirical verification, even if the auxiliary hypotheses imply questionable premises. We discussed this point in connection with one of the most influential of these ideas – Wheeler's sun-streamlined-hypothesis; on Wheeler's hypotheses see also chapters 3 and 6 in main thesis.

(f) Views on climatic and environmental changes as crucial factors in the emergence of first primeval man adapted to open plains were already popular long before the foundation of modern palaeoecological research. As we saw, research in this field was strongly biased by the savannah scenario. It will be important to carry out future investigations on the exact role palaeoecological research played in early and modern attempts to corroborate ideas on human evolution. The results of these investigations can be used to improve an important task in this research: the evaluations of the different models proposed to contextualize early hominin evolution, instead uncritical corroborations of established scenarios, as often done in late 19^{th} and early 20^{th} century.

(g) The reception of alternative ideas for the savannah scenario can only be understood from a historical perspective. I assume that alternative models were often rejected, on one hand because of the belief in empirical corroboration of traditional ideas or on the other hand because it was simpler to detect flaws in these alternative ideas than to apply the same degree of criticism towards traditional scenarios. As shown before, the process of falsifying the aquatic hypothesis has strongly influenced how researchers approach the topic "role of water in early hominin evolution", leading to the neglect of several fundamental aspects of this discussion.

APPENDIX E – RABAUD: A PRECURSOR OF COMPARATIVE PHYLOGENETIC METHOD?

E.1 Introduction

In his succinct review of the history of comparative studies, Mark Ridley wrote:

> The comparative method of 1950 was indistinguishable from the comparative method of 350 BC. The discovery of natural selection has injected a new interpretative principle, but no advance in method. Over the years many an unrigorous practitioner has tried his hand at the comparative method, and they have been following, of course, by exaggerating critics. But neither will be providing our theme. We shall not be reviewing comparative biology. We shall instead be attempting to develop a comparison as a method of studying adaptation. (Ridley 1983, 6)

Ridley's statement on an alleged stagnation of comparative method during 2300 years implies a non-negligible oversimplification, taken into consideration the bulk of adaptive investigations carried out since 1859 – several of the generalizations presented in this chapter are still valid in modern biology. (Ridley' statement is understandable in the context of this time, when the crisis of the adaptationist programme was at a peak. The increasing use of cladistics studies and the rigour of statistics where regarded as important enough to justify a statement which implied that uncountable investigations carried out before 1950 were merely part of a long period of stagnation in the study of adaptation.) On the other hand, some philosophers of science expressed doubts concerning the term *method* in connection with the *comparative method*, as Mahner and Bunge:

> Many biologists claim that there is another very important general method in biology, the so-called *comparative method*. However, there is no such thing as the comparative *method*. Indeed, although the comparison between two or more things may be methodical (orderly) rather than erratic, it is not ruled by a method by its own. That is, there is no set of general rules for comparing things in some respects. (Mahner & Bunge 1997, 77)

It is interesting to see that Ridley regarded the French zoologist Étienne Rabaud (1868-1956) as a precursor of the comparative method. After quoting a sentence by Rabaud (fully quoted below, beginning with "Limited to the comparison of organisms"), Ridley wrote:

> Rabaud is a lonely, isolated figure in the history of research of convergence [...] He inspired no tradition of research on convergent adaptation. But for the fact that he presented no quantitative summary of his conclusions he had the entire comparative method of the early

> nineteen-sixties. It is this comparative method that, after re-stating in abstract form, we are going to develop in the next section. (Ridley 1983, 9)

I do not agree with his evaluation of Rabaud's views on adaptation. It seems that Ridley based his evaluation on Rabaud by focusing on the apparent similarity between Rabaud's criticisms towards oversimplifications and bias in the evaluation of adaptive features and similar statements formulated by modern proponents of phylogenetic approaches to adaptation. We will see that this similarity, although apparently striking, is however mainly superficial. As it will be argued, the main aspect of Rabaud views on convergence is the use of Cuvier's correlation of parts as a straw man to propagate his own neo-Lamarckian ideas.

E.2 Rabaud on Cuvier's correlation of parts

Étienne Antoine Prosper Jules Rabaud began his career investigating human anatomy and physiology and vertebrate teratology (Rabaud 1899; Rabaud 1903). Later in his career he published behavioural and anatomical studies using a comparative approach (Rabaud 1911; 1922; 1925; 1942; 1953). In his publications Rabaud defended neo-Lamarckian views on adaptation, stressing the need of considering behavioral traits in functional analyses and criticizing different aspects of views expressed by Cuvier and contemporary zoologists who adopted a Darwinian perspective (natural selection) in hypotheses on the evolution of traits. Rabaud's work is interesting for different reasons. Firstly, he is one of the few biologists who dedicated a whole book on the phenomenon of convergence. Secondly, in his investigation on convergence he treated several aspects of Cuvier's principle of correlation; finally, as stated above, Rabaud is occasionally mentioned today as a precursor of modern ideas on adaptation as an early critic of what he believed to be anthropocentric and tautological aspects of the work of other biologists.

Although Rabaud recognised Cuvier's contribution as an improvement compared to the work of his predecessors, he criticised Cuvier's methods based on morphological studies to reconstruct "everything else" (*et prétendant tout en tirer*) – i.e., the mode of life of the organism studied (Rabaud 1925, 11). One of Rabaud's main arguments was that convergent traits are not always identical; he attributed to Cuvier a deliberate choice of single features to promote his hypotheses, on the other hand he accused Cuvier of ignoring features which were contradictory to them.

For example, Rabaud criticised Cuvier's use of the law of correlation concerning the digestive tract of ruminant herbivores, which share adaptive features like hoofs, flat molars and

multiple stomachs. Rabaud pointed to the fact that these features cannot be found in the same combination in other herbivores, and concluded that the error in the method is striking (*L'erreur de méthode est ici tout à fait frappante*) (Rabaud 1925, 123). He pointed to several divergencies within convergent species (for instance, several predatory insects capture their prey with the forelimbs, while others capture it with the mandibles) to show that what they have in common is not the form, but in fact the process of nutrition (Rabaud 1925, 142).

Rabaud's criticism is insightful, as he ignored the positive aspects of Cuvier's principle, which are related to the interpretation of the possible function of organismic features through the implicit use convergent traits. A basic aspect in the principle of correlation of parts is related to the fact that organisms of a certain taxon share common traits (in today's terminology: due to common ancestry), what makes possible to infer from features available in a specific fossil evidence on the existence of other features, not available in the fossil record. On the other hand, the existence of certain traits pointing to an adaptation to a certain environment makes it possible to infer other features in the same organism, even if these features are also not available in fossil records. Cuvier's ability to interpret fossil organisms based on this principle showed that it was useful, and this principle is still implied in the way how modern paleontologists infer the putative function of characters found in fossil organisms. In a certain sense, in his attempts to corroborate his criticism of Cuvier as deliberate choosing single features to promote his hypotheses, Rabaud was doing exactly what he accused Cuvier of doing – , but by beginning at the other end.

For instance, returning to Rabaud's assumption that other herbivores do not develop the same traits as ruminants (see above), he listed suids and rodents as "herbivores" (Rabaud 1925, 123). Quite apart from the fact that Cuvier did not imply that all herbivores have to develop the same traits as ruminants (he could not, since he was not an evolutionist), Cuvier, as a skilled comparative anatomist, would certainly not have any difficulties in pointing out the obvious fallacy of Rabaud's arguments related to the suids as herbivorous, since they are, in fact, omnivorous, an adaptation which is also evident in their teeth. As pointed out by Prothero and Schoch when referring to living members of this taxon:

> These animals are mainly omnivorous, eating a wide variety of foods, including fruits, roots and tubers, fungi, ferns, grasses, and even insects, earthworms, and occasional carrion and small vertebrates (such as frogs and mice, if they can catch them). This generalized, omnivorous diet means that their teeth cannot become too specialized for meat slicing or plant

> grinding. Instead, all of these animals have low, rounded cusps on their teeth, which are suitable for many purposes. (Prothero & Schoch 2002, 26)

A similar criticism could be formulated on the fallacy of Rabaud's comparison the dentition of rodents (specialized for gnawing) with the dentition of grazing animals.

One clue to understand Rabaud's criticism can be found in his treatment of a famous example of convergence: the non-homologous (or, to be more precise, the deep-homologous) eyes in different taxa. He pointed to differences in the morphology of the eyes in different taxa, admitting convergence to a certain degree (Rabaud 1925, 156). However, for Rabaud this similarity was not an example of convergence, but "the morphological translation of a fundamental property of the living substance"[262] (Rabaud 1925, 157). This statement is rather obscure, and suspiciously similar to non-Darwinian concepts of this time, as typically expressed by naturalists defending orthogenetic or vitalistic factors in evolution. Apart from the eyes, Rabaud regarded all other cases of convergence as superficial and meaningless for the purpose of the analyses of form/function (Rabaud 1925, 158). Using lengthy comparisons between plants, predatory insects, aquatic vertebrates and flying animals, Rabaud defended the view that morphology alone is inappropriate to reconstruct the way of life of organisms. He stated that there is no necessary relationship between form and way of life (Rabaud 1925, 150) – a highly surprising statement given the innumerable examples of organismic adaptation. More precisely, he stated:

> Limited to the comparison of organisms living in analogous conditions, morphological convergence seems inevitably link to these conditions; but it is evident enough that the conclusion precedes the comparison, instead of following it. The result changes entirely when the comparison is carried out in a complete fashion, when similar forms are placed according to their manner of life, and when these are contrasted with all forms which coincide with them. An objective observer understands well in these cases that the determined conditions of environment do not impose a determined form. (Rabaud 1925, 150, my translation)

Rabaud stated that the emergence of evolutionary ideas did not change the focus on morphology by researchers in his time, and he regarded it as irrelevant for his concepts if the influences on organisms came directly from the environment or from natural selection (Rabaud 1925, 11). However, within evolutionary concepts, there is no opinion that convergent features have to be identical and include all parts of convergent species. The very

[262] Il ne s'agit donc pas seulement d'une convergence morphologique ou fonctionnelle, mais de la traduction morphologique d'une propriété fondamentale de la substance vivante.

examples that Rabaud used to show the alleged mismatch between form and function (prehensile appendices in predatory insects, fish form of aquatic vertebrates, flying animals) belong to the most quoted examples of convergent evolution since decades and are used to give a strong indication for adaptive evolution. Rabaud had a point in stressing the necessity of considering organisms as a whole, including behaviour and environment when reconstructing their way of life, but to make this point it was not necessary to dismiss the relevance of morphology.

Rabaud assumed that it is not possible to "analyze a morphological arrangement [*disposition morphologique*] without studying carefully every detail of it, as well as the whole organism, the function of the examined traits and the ethology of the organism of interest" (Rabaud 1925, 13). He is absolutely correct in this point – this holistic aspect of adaptive analysis was also central in the works of Othenio Abel, Hans Böker and other naturalists in this time (see Appendix C). However, this critique can barely be directed to Cuvier's methods: as one of the most important pioneers of a scientific palaeontology and comparative anatomy Cuvier was obviously aware on the fact that fossils studied by him belonged to organisms once interacting with different aspects of their environment.[263]

It is Rabaud's specific focus on Cuvier's exaggerated statements that explains why he could write that "There is no necessary link between aquatic life and fish form [*nullement rapport nécéssaire*], but this is pure coincidence" (Rabaud 1925, 147). This statement sound so wrong that the question imposes whether we understood him correctly. However, Rabaud really meant it. His attempt to corroborate the above statement on the alleged lack of a relationship between form and way of life reveals the real reasons for his attack of Cuvier's ideas: Rabaud stressed the behavioural components acting as initial factors in the organismic evolution. This idea was illustrated by rather naïve examples. For instance, according to Rabaud, animals conduct a way of life to which they "feel attracted" no matter which form they have or sometimes despite of their form. This idea is interesting, since it consider the fact that organisms change their way of life, and by doing so, they have to use the physiology, anatomy and behavior fine-tuned in connection with other habitats. However, the naivety of his concept becomes clear when Rabaud give the example of snakes climbing trees, explaining that they do so even if they have no legs to perform the function of climbing (Rabaud 1925, 149). He claimed that behaviour has to precede form, illustrating his argument with examples

[263] It is nearly redundant to emphasize that - to use the example above of *Pterodactylus* – Cuvier was able to infer correctly the flying anatomy of these animals by envisaging them as using the forelimbs as wings, which is obviously a behavioral aspect of these creatures.

on secondary aquatic adaptations in vertebrates. According to him, these organisms adopted a life-style before the evolution of morphological traits related to this life. Again, although this statement *per se* is not wrong, what is erroneous is Rabaud's insistence in ignoring the simple fact that Cuvier did not assume that secondary aquatic organisms' morphology evolved before the invasion of aquatic environments (as already stated several times and probably well known by Rabaud, environmental changes and corresponding modifications of anatomy did not belong to Cuvier's paradigm). Rabaud was so involved with his alleged contradiction of Cuvier's idea that he did not recognize the degree of naivety in the following example given to illustrate his argument:

> This attraction [to water] cannot be secondary to the acquisition of the fish form. Nowhere can we see the morphological preadaptation because it is difficult to imagine an animal acquiring the form of a whale out of the water and making a certain way over land before encountering the sea. (Rabaud 1925, 147, my translation)

Instead of this, he envisaged this passage from land to water as follows:

> Among the mammals which, under influences impossible to be precise about, have lost their forelimbs and acquired flippers [?], only the ones which were already in water could survive. As we saw, the modification was not an advantage to them, but the fact that they already lived an aquatic life rendered the modification less detrimental to them. (Rabaud 1925, 147, my translation)

The above statement is in all respects an extremely weak way of reasoning from a modern point of view. However, it is important to note that Rabaud was arguing from an anti-Darwinian perspective common in this time. Although some of Rabaud's arguments towards an integration of ethology and ecology in the morphological analyses[264] (Rabaud 1925, 142) or his critique towards oversimplified views on the role of natural selection (Rabaud 1922, 18-30; Rabaud 1953, passim) might sound apparently modern, this impression apply only to an isolated view of single statement. On the whole, however, his arguments are based on rather simplistic arguments.[265]

[264] Interestingly, Rabaud called this approach the "biological method" (*la méthode biologique*) (Rabaud 1925, 13), a similar term as used by Hans Böker "biological anatomy" to designate a method in which the same claims of integration were made (see Appendix C); this is not a coincidence, since in this time the expression "biological" was often used in the sense of "ecological".

[265] For instance, in his book *Le hasard et la vie des espèces*, Rabaud discussed several topics related to adaptation (mating, interspecific competition, antipredator adaptation) to reach to the conclusion that natural selection is an anthropocentric hypothesis, since it in his opinion based on human views on competition (Rabaud 1953, 231). A close look to his views reveals that he misunderstood completely the concept of natural

However, as explained above, an analysis of the whole work reveals that this similarity is only apparent. Rabaud's ideas on changes of behaviours affecting the course of evolution were already defended by known naturalists, as for example by James Mark Baldwin (1896; 1897), Conwy Lloyd Morgan (1896) and Henry F. Osborn (1896). After the modern synthesis, the concept – commonly known as "Baldwin effect" or "organic evolution" – was further developed by other authors, as for instance Alister Hardy (1965).)Also Rabaud's calls for an interdisciplinary approach in the evaluation of adaptive features was not an isolated phenomenon in this time, as it was propagated by several other early naturalists, as for instance Carl Bergmann, Rudolf Leuckart, Othenio Abel, Hans Böker, Richard Hesse, Franz Doflein and others (see Appendix C).

To summarize, Cuvier's principle of the correlation of parts was not an attempt to evaluate adaptive traits from an evolutionary perspective (again: he was not evolutionist), but an attempt to justify the still valid view that several organismic features are often part of what seems to be an organized and functional whole. The basic idea of Cuvier's principle is valid as a general concept in functional-adaptive analyses, but is invalid in Cuvier's often quoted statements in which he exaggerated the heuristic power of this principle. Modern biologists are usually aware that Cuvier's exaggeration of the explanatory power of the principle of correlation of parts is among others related to the fact that he was not working with evolutionary concepts; but they prefer to ignore this fact and stress the positive aspects of Cuvier's work. We saw that Rabaud not able to do the same, as used Cuvier as a straw man to emphasize his own neo-Lamarckian ideas; he followed a similar approach in his attacks of Darwin's natural selection. On the other hand, Rabaud carefully avoided the topic of problems of interpreting function from fragmentary data, as typical for fossil organisms, since this is exactly one of the most important practical uses of Cuvier's correlation of parts. The apparent similarity between some of Rabaud statements (where he doubt on the validity of hypotheses linking organisms with certain environments) and statements expressed by modern biologists, although quite amazing, is only superficial, and does not have any support to his arguments taken as a whole.

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selection. For him, Darwin's natural selection means a literal "fight" between two individuals (Rabaud 1953, 233-235)! And since an individual cannot "fight" against the environment, the whole concept has to be replaced by his own system (which means: a neo-Lamarckian view of organisms interacting with its environment, in which competition might occur, but is not essential). His ideas on the importance of environment were already exposed in previous works, as for example in *Le transformisme et l'expérience* (Rabaud 1911) and *L'adaptation et l'évolution* (Rabaud 1922).

APPENDIX F: WESTENHÖFER'S LIFE AND *AQUATILE HYPOTHESE*[266]

F.1 Biographical sketch

F.1.1 Professional training

The German pathologist Max Westenhöfer (short for Maximilian Joseph Johann Westenhöfer)[267], (1871-1957), was born in Ansbach (Bayern) as one of eight children of the grammar school teacher Johann Westenhoffer and his wife Johanna, née Knell. He studied medicine at the königlichen medizinisch-chirurgischen Friedrich-Wilhelm-Institut in Berlin (later Kaiser-Wilhelm-Akademie für das militärärtzliche Bildungswesen) from October 1890 until February 1895; afterwards he followed a military career. In 1894 he received his doctorate *summa cum laude* in Berlin for *Tabes dorsalis und Syphilis*. From February until October 1895 he was junior assistant at the Charité in Berlin, in September 1896 he passed his state examination and became an assistant doctor. He served in the infantry in Strasbourg and at the Ulanes in Strasbourg and Hagenau; in March 1899 he was promoted to a senior physician. An important step in his career was a call to the Pathologisches Institut der Universität Berlin, where he was engaged as assistant from October 1900 until 1904. Between 1905 and 1907 Westenhöfer was engaged as prosector (i.e., preparing specimens for dissections for teaching purposes) at the hospital Moabit in Berlin; in September 1907 he accepted the position of an associate professor.

F.1.2 The years in Chile: Westenhöfer as pathologist and "*pago de Chile*"

An important factor in Westenhöfer's interest in anthropology was his activities in Chile, where he spent several years. He went first to Chile in 1908 to establish a pathological institute along German lines. Westenhöfer was a diligent pathologist and a great teacher – highly regarded by his students. Today, his work in Chile is considered to have been of great importance to the country's development of healthcare. Nevertheless, this stay was obscured by two negative events, which influenced Westenhöfer's career both as a pathologist and anthropologist in Chile.

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[266] This summarised biography is based on an unpublished MD thesis on Westenhöfer's anthropological ideas (Bender-Oser 2004a). For a biography in Spanish that further analysed Westenhöfer's activities as pathologist in Chile see (Wicke 1958a; Wicke 1958b).

[267] Westenhöfer's publications until 1913/1914 were signed as "Westenhoeffer" but afterwards as "Westenhöfer". In Chile his name was written in several versions (Máximo, Maximiliano, Westenhofer), see (Wicke 1958a)

On the one hand, Westenhöfer committed a serious mistake during an autopsy of the burned body of a person who was believed to be Guillermo Beckert Frambahuer, the clerk of the German legation in Santiago de Chile. In the first autopsy carried out by Chileans it was decided that it was not possible to determine if the person was murdered or not, due to the fact that the corpse was badly burned. The German legation engaged Westenhöfer to make a second autopsy. He saw this as an excellent opportunity to show his competence as a German scientist (at the time forensic doctors had to be self-taught as there were no courses of instruction). In an attempt to demonstrate his superiority concerning scientific affairs, Westenhöfer openly criticised the first autopsy performed by his Chilean colleagues and carried out the second autopsy with great care and detail. Unfortunately for him, he did not pay enough attention to the identification of the body. It turned out that the dead person was Exequiel Tapia, the legation's servant. With great creativity and criminal energy, Frambahuer had manipulated the evidence to make everyone believe that the dead person was himself, while he escaped with the legation's money. A Chilean dentist, Dr. Valenzuela, observed that the corpse had a complete set of teeth, different from Frambauer, who had artificial teeth. After Valenzuela made this information public, Frambauer was caught and executed. This case was an excellent opportunity for Westenhöfer's enemies (Chilean doctors who were criticised by Westenhöfer or who saw him as an uncomfortable concurrent) to present him as an incompetent scientist.

The second case which seriously damaged Westenhöfer's reputation began in 1911, when Westenhöfer made some blunt (but essentially correct) statements about the poor hygienic conditions in Chile in a German journal. After one of Westenhöfer's students translated these statements into Spanish, many Chileans felt that their national dignity had been offended, giving rise to a huge public controversy about him in which he was characterised as having a strong xenophobic attitude. This case was covered by most newspapers (in Westenhöfer's estate papers there are more than 50 articles published in Chilean newspapers about this case), where he was denoted with the pejorative term "*pago de Chile*"[268]. Demonstrations for and against Westenhöfer were organised. In one of these demonstrations (pro Westenhöfer)

[268] A *„pago de Chile*" is a person behaving in an ungrateful manner towards the Chilean people. In *Diccionario ejemplificado de chilenismos* (Morales Pettorino et al. 1986, p. 3222) the following definition of the term is: "Actitud desagredecida de Chile o de aiguna institución chilena para con sus buenos servidores". This expression was repeatedly used in connection to the alleged German author (actually a Swiss national) of the defamatory book *El ultimo Rincón de Mundo* (Malsch 1907).

organised by the *Federación des Estudiantes* and through the *Congresso Social Obrero* it was estimated that about 12'000 students and workers participated. But the pressure against Westenhöfer was too strong, and he did not have any alternative but to quit his job and return to Germany in August, 1911.

Between 1911 and 1929 Westenhöfer worked in several hospitals and institutes in different functions. In 1917 he received the title of Extraordinary Professor at the University of Berlin, where he was given emeritus status in 1929. Interestingly, Westenhöfer was still very popular among his Chilean students, and they did not forget him. By the late 1920s, some of these early students held influential positions in Chile, and they helped Westenhöfer to return to the country. In 1928 he began to negotiate a new contract with the Chilean authorities and in 1930 he returned to Chile with different aims: to establish pathological institutes in the country, to combat several serious illnesses like tuberculosis and syphilis, and to train new pathologists. He was very well received by Chilean physicians and his former students – even the newspapers wrote about the return of "Don Màximo" – the "*pago de Chile*" was rehabilitated.

Unfortunately, Chile had financial problems at the time and was not able to pay Westenhöfer and other foreign professors. Therefore, he returned to Germany in 1933 and only finally returned to Chile in 1948, following an invitation by the Chilean ministry of public health to spend his old age in Santiago de Chile. He died in Santiago de Chile on 25th September 1957 at the age of 86 years.

F.2 Westenhöfer's *Aquatile Hypothese*

Besides his ideas on the alleged primitivity of human phylogeny (see Appendix D), Westenhöfer developed a further hypothesis on human evolution, that he called "*Aquatile Hypothese*". Westenhöfer did his first observations leading to this hypothesis in 1909 -1911 in Chile while he studied the anatomy of indigenous populations in this country. He observed a frequent variation of internal organs, among others what he believed to be an "atavistic" appendix and a lobulation of the spleen and kidney. He called these three anomalies "*prognonische Trias*", and thought that he discovered a new racial feature. However, in his further dissections in Germany, he found similar features in European individuals. In comparative anatomical researches he saw that lobulated spleens and kidneys are not unique human features, but also common in some aquatic mammals. This observation was the starting point for his first speculations on a semi-aquatic phase in human evolution. He believed that the incomplete unification or consolidation of spleen and kidney in humans is only exceeded by cetaceans. He was convinced that concerning the kidney, it is only exceeded

by the cow, the pinnipeds, the sea otter and bear, the hippopotamus and the rhino, all animals that are semiaquatic or aquatic today or are believed to descend from aquatic animals. Interestingly, Westenhöfer did not give any references to corroborate the statement that the bear and the rhino are believed to descend from aquatic animals. He regarded it as possible or even probable that this strange similarity between very different groups of animals is the result of a convergent evolution. Consequently, so Westenhöfer, "the fact that these animals all have a similar way of life leads to the conclusion that also in the human line there was a mammal adapted to an aquatic way of life" (Westenhöfer 1923, 1252, my translation).

One year later Westenhöfer published another paper in which he discussed further human features that in his opinion are connected to an aquatic past:

> We have to imagine human ancestors living in an environment in which the dentition is needed to grasp and triturate the food, but the demand connected to the capture of the prey should not be too high. All the functional demands of the dentition have to be very different from those of primates living in forests. A mammal living in water would find an environment in which a stronger development of the dentition is not needed because of the relative softness of the food. (Westenhöfer 1924, 259-260, my translation)

Westenhöfer does not give details of the specific anatomical modification of the dentition. However, he was more precise concerning the reduction of body hair and great amount of subcutaneous fat in humans and aquatic mammals. In the same paper as above he wrote:

> The fact that the human body is rather hairless, but once was surely covered by a fur, can be seen in analogy to the relative hairlessness in aquatic mammals (whales, seals, rhino, hippo)[269], especially if considered that there is no other plausible explanation so far. Furthermore, the human predisposition to accumulate great amounts of subcutaneous fat (a feature which is obviously already present in pre-civilizations – I remember the so called Venus of Bassompière [sic, Westenhöfer meant the Venus of Brassempouy] would be consistent with the above idea. (Westenhöfer 1924, 260-261, my translation)

In several other papers and in two books Westenhöfer added further arguments to his aquatic hypothesis, like bipedalism connected to swimming and diving, the reduction of olfaction, the face-to-face copulation, swimming and diving skills the development of the brain, the form of

[269] Although Darwin was not quoted by Westenhöfer in this specific context, it cannot be excluded that the first insights on the *Aquatile Hypothese* were directly or indirectly inspired by Darwin's ideas. Darwin, when discussing the hair reduction in humans in his *Descent of Man*, noted that a naked skin and a large amount of subcutaneous fat are features of a number of aquatic mammals (Darwin 1871, vol. 1, 148).

the hand, foot and ear, some specific skin glands, and the hair tract in the lower arm; see references in Bender-Oser (2004a, 80-93). Westenhöfer went through the literature of his time and quoted any author who wrote something about "aquatic features" in non-human primates and humans. He did it without much consideration on the quality of the arguments of the quoted works or the lack of internal logic between the different ideas. For instance, Westenhöfer quoted G.L. Sera (Westenhöfer 1942b, 311) to corroborate his own aquatic hypothesis. However, Sera did not write about a semi-aquatic past of humans, but about alleged aquatic features of South American primates; for a detailed analysis of authors quoted by Westenhöfer see Bender-Oser (2004a, 93-98).

Another example of the lack of inner logic in his attempt to corroborate the *Aquatile Hypothese* is supplied by his reference to a paper written by Bruno Henneberg on the anatomy and physiology of the ear. In 1909 Henneberg published a paper based on comparative anatomy of several terrestrial mammals in which he tried to demonstrate that in these mammals the auricula shows rudiments of an early adaptation to an aquatic life, more specifically, to close the ear canal during submersion (Hennenberg 1909, quoted in Henneberg 1942). More than three decades later he published a paper in which he tried to demonstrate that the human ear-anatomy also must have had the same ability in the past, without giving precise indication of the time in which such a development may had occurred (Henneberg 1942). Motivated by Henneberg's prompt to find persons with ears provided with contractible muscles, Westenhöfer claimed to have searched and found such a person (Westenhöfer 1935, 72-73). He was convinced that his *Aquatile Hypothese* has become less speculative through this new evidence (Westenhöfer 1935, 72-73).

A last example of Westenhöfer's lack of care in his argumentation is supplied through his statements on hair tract. Westenhöfer was aware that in human beings and other anthropoids – as well as in other primates and quadrupeds – the hair tract points towards the elbow on the lower forelimb. Since this feature is common in most mammals, he could evidently not use it as an argument for his *Aquatile Hypothese* (he normally used arguments related to unique features in humans when compared with apes). However, he simply overlooked this detail and stated that "I would see it [the hair tract in the forearm] as not insignificant support for my *Aquatile Hypothese*, since such a direction of the hairs on the lower arm during swimming stretching the arms forward would have been useful" (Westenhöfer 1942b, 311). For a detailed analysis of Westenhöfers' *Aquatile Hypothese* and the works used for its corroboration see Bender-Oser (2004a). In following Table (F.1) the arguments of

Westenhöfer's *Aquatile Hypothese* and Hardy's aquatic hypothesis (AH) are summarized and compared; on Hardy's AH see Appendix D).

Westenhöfer encountered great difficulties in the attempt to conciliate his primitivity hypothesis and his aquatic hypothesis. This difficulty was based on the conceptual differences between the two models. The aquatic hypothesis required the acceptance of convergent evolution, i.e. implying a classical view of Darwinian evolution based on variation and natural selection. This model was incompatible with the argumentation of the primitivity hypothesis, which was strongly interwoven with Westenhöfer's belief in Platonic idealism. In fact, Westenhöfer regarded human beings as "essentially unchangeable" over time. This explains why Westenhöfer believed that a bipedal reptile was "already human". In his mind, just the external appearance can be modified (due to the realization of hidden potentialities of the "essences"), but not the human essences themselves. As strange as this idea might sound today, Platonic idealism was a popular philosophical concept until Karl Popper's influential criticism against it. The incompatibility of Westenhöfer's ideas was probably the main reason why Westenhöfer did not mention the aquatic hypothesis in his last book of 1948.

Table F.1 Comparison between *Aquatile Hypothese* and AH

Arguments for a semi-aquatic phase in early hominin evolution	Westenhöfer	Hardy
Subcutaneous fat is indicated as an important divergent feature and interpreted as an analogy between humans and aquatic and semi-aquatic vertebrates, developed to prevent heat loss in water	yes	yes
Subcutaneous fat to improve swimming performance by making human body more streamlined	no	yes
Human ability to swim at the water surface and under water indicates a semi-aquatic phase in early hominin evolution	yes	yes
The strong reduction of body hair in humans is interpreted as analogous feature to aquatic and semi-aquatic mammals	yes	yes
The lobed spleen and kidneys of humans are regarded as important distinctions between humans and great apes and interpreted as adaptations to an earlier semi-aquatic lifestyle in human phylogeny	yes	no
Great development of the human brain and of some aquatic mammals is associated with an aquatic life	yes	yes
Upright posture is interpreted as an adaptation to a semi-aquatic environment	yes	yes
The divergence in the hair tract in the body between human and apes is interpreted as an adaptation to swimming. Such an arrangement of hair offered less resistance in water and may have been a first step in aquatic adaptation before the hair reduction.	no	yes
The hair tract on the forearms is regarded as an adaptation to swimming (to reduce water resistance when stretching the arms forward)	yes	no
The sensibility of human hands developed in connection with to collect organisms under water	yes	yes
Tool-making began in a semi-aquatic environment	yes	yes
Gap in fossil evidence is probably related to the fact that fossil evidence should be searched in coastal environments	no	yes
Humans like to go to the seaside and spend time in water (bathing, and play in water)	no	yes
Great availability of protein-rich foods is regarded as a strong argument for a semi-aquatic life in early hominin evolution	no	yes
The face-to-face copulation is regarded as convergent to the face-to-face copulation in aquatic mammals	yes	no
Regression of olfactory organ (bulbus and lobus olfactorus) is fund in humans and aquatic mammals	yes	no
An early palustrine life (marshes and swamps) of man is regarded as likely	yes	no
Webbed-fingers sometimes found in humans	yes	yes
Beowulf's struggle with the dragon under water is a hint that humans perhaps did live and fight with such dragons in water	yes	no

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