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Bender, Pedro Renato

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

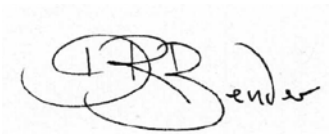
Pedro Renato Bender

A Thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Doctor of Philosophy

Johannesburg, 2014

DECLARATION

I declare that this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.



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4 of August 2014 in Wabern, Switzerland

Abstract

In the present thesis the use of convergence as a tool in functional analyses was investigated, with special focus on comparisons using distantly related species ("convergence approach"). Guidelines for the convergence approach were forumlated and applied in the evaluation of selected hypotheses on the contextualization of early hominins. Additionally, comprehensive reviews on water use in primates were carried out, with special focus on hominoids, including humans. The first description (and video footage) of swimming and diving behaviour in a common chimpanzee (*Pan troglodytes*) and an orangutan (*Pongo pygmaeus*) were presented here, along with swimming behaviour in other great apes (without video footage). Hypotheses on the loss of instinctive swimming in hominoids were discussed and the Saci last common ancestor hypothesis was proposed. This model suggests that the loss of swimming ability in hominoids is best explained as a consequence of phylogenetic constraints linked to the adaptation to an arboreal life in the last common ancestor of this taxon.

Furthermore, several hypotheses on early hominin evolution were reviewed. It was pointed out that several of these hypotheses have similar methodological flaws in the use of analogies to corroborate specific arguments. A hypothesis on the emergence of the habitual bipedalism in early hominins was outlined, arguing that this trait did not evolve in association with a locomotory advantage or for other reasons usually presented in the literature, but as a signal to advertise unprofitability – as a warning signal in an anti-predator strategy. It was argued that fossil evidence does not allow a high resolution of inference concerning incipient traits – traits which are not optimized to fulfil a certain function after a functional change.

The consideration of different lines of evidence presented in this thesis indicate that the topic "water use" must be considered in discussions on early hominin evolution. The fact that humans regularly and intensively interact with water can be considered as an indication that in some part of human phylogeny after the hominin/panin split, swimming and diving ability was specifically selected. However, contrary to the view of several proponents of the aquatic hypotheses, it was demonstrated that humans are not absolutely unique concerning their ability to learn to swim and to dive. It is therefore also conceivable that our ability to learn to swim is associated to our cognitive abilities and is not a product of specific selection in our past.

In memory of my principal supervisor

Professor Phillip V. Tobias

1925 – 2012

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Glossary

This section includes all newly defined or revised terms used in the present thesis (including Appendices).

Biological constellations: The product of methodologically unsound selection of traits to corroborate a preconceived scenario on the evolution of these traits.

Biological implausibility: Refers to the inferences based on weak thought experiments or comparisons between distantly related organisms bearing superficial similarity in traits without considering data on functionality and evidence based hypotheses on the emergence of these traits.

Convergence approach: Method in which non-homologous patterns of similarity between two or more distantly related species are used to infer on the functional focus of the traits under investigation.

Epistemological discrepancies: Taxa or species difficult to place in a single logical category in pre-Darwinian zoological treatises due to their ambivalent anatomy or behaviour.

Functional focus: The total pattern of adaptive and non-adaptive features of an organism which is effectively used or can be used under certain circumstances in its interaction with the environment.

Interlocking point: The stage in which a trait or a set of traits fulfils the minimal preconditions to perform a given function in the phylogeny of an organism.

Swimming: To progress in water by self-propulsive, spatially oriented movements.

Unprofitability hypothesis: A hypothesis on the emergence of the habitual bipedalism in early hominins arguing that this trait did not evolve in association with a locomotory advantage or otherwise as usually presented in the literature, but as a signal to advertise unprofitability – as a warning signal in an anti-predator strategy.

Water use: Behaviours related to an organism's interaction with water. In a strict sense, this term applies to behaviours displayed by an organism when it is inside of water, such as during swimming, diving partially or completely, wading and drowning. In a broader sense, this term also includes behaviours in which an organism does not enter a body of water, such as during drinking, exposure to rain, while crossing a river using natural bridges or playing with water (e.g., water from a hose or water in a tub, with the animal standing outside the tub).

CHAPTER ONE – INTRODUCTION

1.1 General remarks and rationale

The present work investigates the use of non-homologous patterns of similarity (analogous or convergent traits) in the analyses of adaptive features, especially in hypotheses proposed to contextualize crucial phases of early hominin evolution. A further delimitation is the investigation on patterns of water use in primates, with special focus on hominoids, including humans.

Two distinct uses of the term analogy are relevant in the present thesis: on the one hand the role of analogy in cognitive sciences, on the other hand analogous features used in biology to describe patterns of similarity in traits which have not been inherited from common ancestors in the studied species.

1.1.1 The role of analogy in cognitive sciences

William Whewell[1] described humans as "reading the language of the external world, and translating as they read" (Whewell 1847, 42). In this process, inanimate and animate nature is constantly and often unconsciously scrutinized in the search for patterns of similarity and dissimilarity. The recognition of real or imaginary patterns can lead to superstitious beliefs (Valiela 2001, 15), vague assumptions, weak speculations, yet also to valuable hints to solve problems in daily life as well as strong insights which can lead to scientific hypotheses. Since it is long recognized that the use of analogy plays a crucial role in the process of categorization and problem-solving[2] (Forbus 2001; Höffding 1967; Hoftstadter 2001; Holyoak et al. 2001; Koepcke 1971, 9-13; Lorenz 1959a; Riedl 1980, 31-81; Rips 1989; Vosniadou & Ortony 1989).

In cognitive sciences, analogy has been described as a "partial identity" between objects (Mach 1906, 220), or as similarity between different objects concerning certain aspects,

[1] He was perhaps inspired by analogies expressed by Galileo Galilei, who wrote in 1623 as follows: "Philosophy is written in this grand book, the universe, which stands continually open to our gaze. But the book cannot be understood unless one first learns to comprehend the language and read the letters in which it is composed. It is written in the language of mathematics, and its characters are triangles, circles, and other geometric figures without which it is humanly impossible to understand a single word of it; without these, one wanders about in a dark labyrinth" (Galilei 1957, 237-238, transl. by Stillman Drake).

[2] The expression 'analogical reasoning' is a standard one in the specialized literature. However, as Hofstadter aptly pointed out, this term "reveals the bias towards *reasoning* as opposed to simply *understanding*. The idea that people constantly see situations in terms of other situations simply because that is human nature, and not because they wish to solve some problem, is almost totally ignored these days" (Hofstadter 1995, 270).

properties or relations (Löther 1991; Polya 2009). Analogy is used to designate comparisons that share relational information (Gentner *et al.* 2001), or as the ability to think about relational patterns (Holyoak *et al.* 2001). This ability is characterized by the transfer of information from one object (called source or base) to another subject (the target). The target is a problem seeking a solution; the source is a known phenomenon used to understand the target (Holyoak *et al.* 2001 and other chapters in this book).

Several authors emphasized the value of analogies in cognition. Jevons, for example, was convinced that "The whole structure of language and the whole utility of signs, marks, symbols, pictures, and representations of various kinds, rest upon analogy" (1958 (1874), 628), and Polya stressed that "Analogy pervades all our thinking, our everyday speech and our trivial conclusions as well as artistic ways of expression and the highest scientific achievements" (Polya 1973, 37).

Similarly, Hofstadter states:

> In my case, the shift [of view-point] is to suggest that every concept we have is essentially nothing but a tightly packaged bundle of analogies, and to suggest that all we do when we think is to move fluidly from concept to concept – in other words, to leap from one analogy-bundle to another – and to suggest, lastly, that such concept-to-concept leaps are themselves made via analogical connection, to boot. (2001, 500)

It is probably difficult to find an area of ancient and modern scientific discussion in which analogies were not regularly used. Analogy played a crucial role in early Greek thought (Fiedler 1978; Lloyd 1971), in the works of the astronomers Johannes Kepler[3] and Galileo Galilei (Gentner 1982; Gentner et al. 1997); it is implicit in the evolutionary ideas of Benoît de Maillet in the 18th century (see Appendix B) in the comparison between selection under domestication and that under nature stated by Charles Darwin (Evans 1984) and other authors before him,[4] in the construction of the periodic table of elements by Dmitri Mendeleev

[3] Kepler expressed the importance of analogy with following words: "And I cherish more than anything else the Analogies, my most trustworthy masters. They know all the secrets of Nature, and they ought to be least neglected in Geometry" (quoted in Polya 2009, 12).

[4] For instance, a similar analogy was already proposed by the Persian-Khwarezmian scholar Abū al-Rayhān Muhammad ibn Ahmad al-Bīrūnī (973-1048) in his book *India* (from the translation of E. C. Sachau):

> The agriculturist selects his corn, letting grow as much as he requires, and tearing out the remainder. The forester leaves those branches which he perceives to be excellent, whilst he cuts away all others. The bees kill those of their kind who only eat, but do not work in their beehive. Nature proceeds in a similar way; however, it does not distinguish for its action is under all circumstances one and the same. It allows the leaves and fruit of the trees to perish, thus preventing them from realising that result which they are intended to produce in the economy of nature. It removes them so as to make room for others. (Biruni 1910, vol. 1, 400).

(Kedrov 1967), in the comparison between ontogeny and phylogeny (Gould 1977; Kleinsorge 1900), and in the long tradition of comparing structures of living organisms with mechanical instruments (e.g., by Giovanni Borelli, Leonardo da Vinci and William Harvey) to understand principles of movements in animals or to develop or improve human technology . Analogy is used by children (Goswami 1992; Goswami 2001; Inhelder & Piaget 1958), by apes (Oden et al. 2001), by scientists in their daily discussions (Dunbar 2002), in science teaching (Brown & Salter 2010; Glynn 1995), in the development of scientific models (Del Re 2000; Livingstone & Harrison 1981), perhaps by chess players to find strong moves and by chess teachers in their attempts to explain concepts in this game[5], in the creation of imaginary organisms (see, e.g., Dixon 1982; Serafini 1981; Stümpke 1979). Analogy was crucial in the Copernican revolution, for instance in the discussion on the existence of humans on other planets (see plurality of worlds, Appendix B), and it is very common in form of rhetorical figures of speech[6] in everyday talk, in poetry and prose.

1.1.2 The role of analogous traits in evolutionary biology

In biology, the term analogy is rarely used in connection with mental processes, but usually to describe non-homologous patterns of similarity between two organisms which evolved under similar selective pressure. There are different terms to denominate analogous traits in biology (see Appendix C on the historical development of these concepts). The most common term is "convergence" (L. *cum* together + *vergere* to incline). Traditional examples of convergences in biological textbooks are the broadly similar appearance of fast swimming vertebrates from different taxa (porpoises, lamnid sharks, ichthyosaurs, and tuna), the convergent growth forms in desert plants which evolved in Cactaceae, Aschlepiadaceae and Euphorbiaceae, and the wings of birds and bats.

Convergent evolution is a good example of how the same biological phenomenon can have different connotations depending on the goals pursued in different research programs.

These and other sentences were sometimes interpreted as views resembling Charles Darwin's basic ideas on natural selection and evolution (Raïnow 1943). However, this view was rightly criticized by Wilczynski (1959). More detailed sentences which evoke the idea of organic evolution and natural selection can be found in earlier text of an Islamic scholar, namely in the ninth century *Book of Animals* by the Mu'tazili philosopher al-Jâhiz (c. 776-869); see quotation in Zirkle (1941).

[5] See, for instance, Aaron Nimzowitsch's analogies in his famous book *Mein System* (Nimzowitsch 1958, first publ. 1925). There is a long tradition of using analogies in chess literature; see for instance Garry Kasparov's book *How Life Imitates Chess* (Kasparov & Greengard 2007).

[6] Following a standard definition, figures of speech are "forms of expression that depart from normal word or sentence order or from the common literal meanings of words, for the purpose of achieving a special effect" (*Encyclopedia Americana*, vol. 11, p. 195). Known figures of speech are metaphors (Coenen 2002; Lakoff & Johnson 2003; Miller 1996, 219-262), parables and similes. Certain areas of human culture seem to make an above-average use of this type of analogy, as for instance in religious language (Dithmar 1970; Gerhart & Russell 1984; Mollerus 1665; Soskice 1987).

Convergent traits have a negative connotation in systematics – they have to be identified and eradicated from the attempts to reconstruct phylogeny (Lauder 1996; Simpson 1972, 129; Wake 1991, 564). In evolutionary biology – especially when treating organismic features from an adaptationist[7] perspective – several authors recognized explicitly that convergent traits are essential to understand the form-function complex of organismic traits. The use of convergence as a tool has a long tradition in biology. It was already implied in the ideas expressed by several naturalists long before the general acceptance of evolutionary paradigm in the second half of the 19th century. For example, 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. An ancient example of such functional grouping based on convergences was written by the Greek Theophrastus (c. 371-c.287 BC) in his *Enquiry into Plants* (Theophrastus 1916). An intriguing use of convergence as a tool in zoology in the first half of the 19th century is supplied by Cuvier. In 1830, based only on a drawing, he was able to recognize *Pterodactylus* correctly as a flying reptile, in opposition to a popular view in this time of *Pterodactylus* as an aquatic animal (Taquet & Padian 2004). The implicit method used by modern biologists is basically the same as used by the French naturalist: the knowledge on anatomy, physiology and behaviour of extant or extinct organisms is used to infer causality and functional significance of features from other extant or extinct organisms. This method is a fundamental concept in the present thesis, coined here "convergence as a tool" or "convergence approach."

According to this perspective, the comparison between non-homologous patterns of similarity of a set of species can supply cues to understand factors influential in the evolution of adaptive traits (Bender 1999; Currie 2013; Hickman 1988; Koepcke 1971; Koepcke 1973; Lorenz 1974; McGhee 2011; Mooney et al. 1977; Remane 1943; Simpson 1972, 132; Vogel 1998b; Wickler 1971a; Wickler 1972). Convergent traits reflect the concept of symmorphosis, which predicts that economy of resources is essential at all levels of organismic organization and that biological structures should be matched to functional requirements (see Weibel 1998 and other chapters in the same book). Cuvier (1831b, vol. 1, 4) regarded the process in which convergences emerge (he did not explicitly use the term "convergence ") as analogous to the process of experiments carried out in laboratories, a view occasionally also expressed by modern biologists (see, e.g., Gould 1976; Orians & Solbrig 1977a). Studies focusing on

[7] Until further notice, the term "adaptation" follows the classical definition of a trait or set of traits which increases the reproductive success (fitness) of its possessor.

interspecific non-homologous patterns of similarity are known under several terms, such as "comparative method" (also called "phylogenetic comparative method") (Harvey & Pagel 1991; Martins 2000; Martins & Housworth 2002; Pagel & Harvey 1988; Ridley 1983), "convergence approach/*Konvergenzforschung*" (Bender 1999; Coddington 1994; Wickler 1971a), and "likelihood approach" (Baum & Donoghue 2001). In ecology, as stated above, the study of life-forms (or functional types, or functional groups) (Gitay & Noble 1998; Koepcke 1971; McGhee 2008; Raunkiaer 1934; Remane 1943; Remane 1951) is intrinsically related to the concept of convergence as a tool.

1.1.3 Convergence as a tool in hypotheses contextualizing early hominin evolution

Modern humans are undoubtedly unique concerning several aspects of their biology[8]. This is true regarding the amount and the complexity of cultural and cognitive developments, such as complex language (Deacon 1997; Kirby 2007; Pinker 1994) or sophisticated technology needed to adapt to new environments (Wallace 1895, 174-175). However, as argued by Foley, "uniqueness is paradoxically a characteristic of all species, not just humans" (Foley 1987, xvi). Given the numerous examples of convergences in the organismic world, it is justified to assume as a working hypothesis that early hominins were not unique in their several anatomical, physiological and behavioural traits, but developed adaptive features which are comparable to other organisms which evolved under similar selective pressures. In fact, some early and modern palaeoanthropological hypotheses use implicitly or explicitly convergence as a tool in their main argumentation. Especially important in this context are the savannah hypotheses, which traditionally explained crucial early hominin features as adaptations to open environments. These models held strong influence on research in palaeoanthropology for decades and are still influential. Within the theoretical framework of the savannah hypotheses, several authors proposed auxiliary hypotheses in which early hominins were presented as analogous to other savannah organisms (Cachel 2006; Hilzheimer 1921; Jolly 1970; Jolly 2001; Matthew 1950 (first publ. 1915)).

Interestingly, although savannah hypotheses have been challenged in recent years, several critical aspects are still understudied (Bender 1999; Bender et al. 2012). Among these, scientific corroboration of early and modern savannah hypotheses is largely neglected by historians of science and by practitioners.[9] Furthermore, the interplay between empirical

[8] A collection of comparative information regarding hominoids, with an emphasis on uniquely human features, are presented in *The Matrix of Comparative Anthropogeny* (MOCA) from the *Center for Academic Research and Traning in Anthropogeny* (CARTA) (see http://carta.anthropogeny.org/moca/topics).

[9] The reason for this neglect is largely historical. Palaeoanthropologists and historians of palaeoanthropology often associate the emergence and corroboration of the savannah hypotheses with the first description of

evidence and the use of analogies hypotheses used to contextualize human evolution is poorly understood. This important topic applies central issues to the scientific debate on early hominin evolution, as it relates to (a) the evaluation and prediction of the varying arguments of the savannah model; (b) the role of a possible confirmation bias in the development of the savannah model; and (c) the influence of the savannah model in the reception and formulation of alternative hypotheses on early hominin evolution.

A further aspect of the use of convergence as a tool in palaeoanthropological hypotheses concerns the role of specific alternative hypotheses on early hominin evolution called "aquatic hypotheses" (or aquatic ape theory, or aquatic ape hypothesis). Although the aquatic hypotheses were strongly criticized by palaeoanthropologists and some researchers probably feel that further discussion on this subject is superfluous, there are good reasons for a closer investigation of this idea. The most important is that the interaction of early hominins with water bodies is a crucial aspect of palaeoanthropological discussion, independent of any contextualization of early hominin evolution in a semi-aquatic environment. There is no scientific justification for stigmatizing the topic "patterns of water use" in hominoids, including hominins (Bender *et al.* 2012) simply because the issue is negatively associated[10] in palaeoanthropology. Patterns of water use are relevant in evolutionary biology, because how a terrestrial organism interacts with water bodies can have a crucial influence on other factors of its ecology. For example, swimming ability influences strategies used to cross water bodies that act as barriers to dispersal, home range, the exploitation of aquatic food resources and a means to escape from predators or for thermoregulatory purposes (Duplantier & Bâ 2001; Hickman 1977; Kempf 2009; Wilber & Weidenbacher 1961). It is remarkable that extant hominoids (including humans) are not able to swim instinctively – a rare trait among terrestrial vertebrates. Although the lack of innate swimming ability certainly has a strong impact on the dispersal of hominoids, few hypotheses have been formulated addressing this topic (Bender & Bender 2013). On the other hand, humans interact with water in a way which often leads to the development of swimming ability (Bender 1999), an aspect of human biology that is rarely discussed in classical palaeoanthropology; see Appendix D.

Australopithecus africanus in 1925, and are usually not aware on the pre-Dartian (even pre-Darwinian) roots of this idea. This topic is discussed in Appendix D.

[10] In chapter Appendix B another example of topics stigmatization is discussed in connection with the pre-Darwinian evolutionary hypothesis proposed by Benoît de Maillet.

1.2. Overall aim

This thesis investigates the use of analogical reasoning and convergence as a tool in evolutionary biology and its application in hypotheses on early hominin evolution. Furthermore, special consideration is given to hypotheses implying early hominins interacting regularly with water bodies.

1.3 Objectives

(a) To review some aspects of the role of convergent organisms in natural sciences in pre-Darwinian times

(b) To review the emergence of the concept 'convergence' in evolutionary biology

(c) To review the role of empirical evidence and analogies in the formulation of hypotheses on early hominin evolution

(d) To investigate the interaction with water in non-human primates (including hominoids), through a literature review and a questionnaire survey

(e) Collect empirical data on swimming and diving performance in non-human hominoids

(f) To investigate interaction with water within human tribal cultures by doing a database search of the literature

(g) To investigate some aspects of the complex interplay between evidence and hypotheses in palaeoanthropology (with especial consideration of the use of convergence as a tool) and formulate principles and guidelines for the use of convergence as a tool

1.4 Organization of the work

This thesis supplies both reviews of the literature and empirical investigations. Consequently, the different chapters follow different structures of narrative. The chapters treating historical reviews are placed in Appendices in order to improve the flow of the narrative. They follow an approach not unusual in historical analyses by making extensive use of notes for additional information that might be too digressive for the main text. However, in chapters treating empirical evidence, contemporary literature reviews or in which a theoretical concept is developed, the structure of the narrative is the same as used in primatological or palaeoanthropological publications. The specific methodologies used are described at the beginning of the corresponding chapters.

The work is divided as follows:

Chapter 1 is the introduction.

Chapter 2 presents an analysis of chosen aspects of the term convergence and supplies an overview of the use of convergence in the formulation of hypotheses on adaptation in different biological disciplines.

Chapter 3 presents a convergence approach in which non-homologous patterns of similarity between two or more distantly related species are used to infer the functional focus of the traits under investigation. In this chapter guidelines are presented for the convergence approach.

In Chapter 4 a broad spectrum of water use in primates is investigated. Chapter 4.1 focuses on water-contact behaviour in non-human primates. Chapter 4.2 has a special emphasis on water use in hominoids. Chapter 4.3 presents the first description of swimming and diving behaviour in non-human hominoids.

Chapter 5 presents an extensive literature analysis of the broad spectrum of human behaviour regarding water (e.g., bathing, washing, diving, playing, swimming and drowning).

Chapter 6 is the discussion and an application of the convergence approach. The aim of this chapter is the investigation of some aspects of the complex interplay between evidence available to modern palaeoanthropological research and hypotheses proposed to interpret this evidence. This chapter contains also the the conclusion of the thesis.

Appendix A presents an overview of analogical thinking in pre-Darwinian concepts, focusing on the role of convergent organisms (here called “epistemological discrepancies”) in the generation of conflicts in early attempts to classify biological diversity.

Appendix B investigates the paradoxical role of epistemological discrepancies in the emergence of pre-Darwinian evolutionary concepts.

Appendix C outlines the use of convergence as a tool in early attempts to integrate an ecological perspective in comparative anatomy and biogeography.

In Appendix D different facets of the development of savannah hypotheses proposed between 1809 and 1939 are investigated. I discuss the origin and development of the savannah hypotheses and the reasons why these ideas are sporadically related to the work of Raymond

Dart. Furthermore, the use of climatic deterministic statements in the initial hypotheses on early hominin evolution is analyzed.

In Appendix E some specific aspects of the work on convergence carried out by the zoologist Étienne Rabaud are investigated.

Appendix F summarizes Max Westenhöfer's life and work.

CHAPTER TWO: DIFFERENT ASPECTS OF THE USE OF CONVERGENCE AS A TOOL IN ADAPTIVE ANALYSES

2.1 Introduction

The study of adaptation is central to evolutionary biology. Biologists are interested in definitions for adaptations, in the distinctions between adaptive and non-adaptive traits, in the specific ways that adaptive traits evolved, and in the different ways to infer the adaptive role of traits in living and extinct organisms. One of the most powerful tools to understanding the adaptive nature of traits in living organisms and to use this knowledge to formulate hypotheses on the adaptive traits of extinct organisms is to use convergences. This view is clearly expressed in following statement by Steven Vogel:

> Convergence (that is, the independent development of similar design features) should play a more positive role in studies of function. Specifically convergence provides a way to tell features that have important functional significance from features that do not. And the common aspects of the habit and habitat of the organisms involved point to the nature of that functional significance. (Vogel 1998b, 13)

This statement expresses two main aspects of the present thesis: that convergences are crucial studies of adaptation, but the value of convergence as an analytical tool in functional analysis is still not fully acknowledged by a majority of biologists working in this field.

In this chapter I will present the rationale and propose guidelines to the use of convergence as a tool in the study of homoplastic patterns of similarity between species which need not be compared to each other using detailed phylogenetic trees (see below for explanations). The present work does not supply extensive examples of convergences. Examples of convergences were extensively published by other authors (Conway Morris 2008; Koepcke 1971; 1973; McGhee 2011). Koepcke's book (see Appendix C), unfortunately largely ignored even by German-speaking biologists, is the most important work on convergence prior to the discoveries of processes governed by mechanisms deeply conserved across a wide range of species (deep homology). McGhee's book is an excellent source for a description and analysis of the phenomenon of convergent evolution (McGhee 2011). Conway Morris' work, although also providing several interesting examples of convergences, is disappointing in the chapters where he discussed the theological/metaphysical ideas on human evolution in connection with questions of predictability of organismic evolution (see also Appendix D, chapter D.6.2 on

similar metaphysical considerations, for example by the Jesuit Teilhard de Chardin) (Conway Morris 2008).

The chapter begins with a review the modern debate along with the terminology of homology, convergence, parallelism and adaptation. Afterwards the rationale and guidelines for using convergence in the analyses of adaptive traits are formulated.

Diverse historical events linked to the use of analogies in the natural sciences will be presented in the Appendices A, B, C, D, E and F. Justification for these historical investigations being excluded from the present chapter is due to the attempt to link the convergence approach discussion with modern biological debates. Cross-references to the historical investigations from the Appendices are noted in the text.

2.2 Homology, homoplasy, Homoiologie, parallelism and other terms: the difficulties in establishing a terminology valid for different biological disciplines

When referring to homologies, textbooks often stress the importance of recognizing the hidden patterns of homology in organisms of different taxa. The classical example (already used in pre-Darwinian books on natural science) depicts the bones of arms in bats, birds, *Pterodactylus*, whales and humans, revealing a pattern of similarity that can be easily identified, despite the divergences in the lengths of bones or functionality of the forearms in these animals (see, e.g., Romanes 1901, 54-56). The concept of homology has a long and interesting history. The multiple meanings and historical development of the term "homology" and related terms were investigated by several authors (Boyden 1943; Boyden 1947; Donoghue 1992; Haas & Simpson 1946; Hossfeld & Olsson 2005; Panchen 1999); see also Appendix A on misconceptions concerning the classification of secondary aquatic animals in pre-Darwinian period; and Appendix B on the use of wrong classification of these organisms for the emergence of first evolutionary ideas. Modern textbook definitions of homology – in the simplified glossaries – are basically the same as defended by Charles Darwin: homology is defined by common ancestry. However, in recent decades, the discussion on homology in different research programmes has revealed a complex, more nuanced presentation. These research programmes are associated with various fields which tend to carry out their investigations using somewhat different perspectives on homology. The research revealing the most surprising insights is that of evolutionary developmental biology and genetic research. Among the topics investigated, the most important are: (a) structural homology or the study of developmental underpinnings of homologous characters and

processes operating at different levels of biological hierarchies, involving constraints and epigenetic interactions (Hall 1999; Müller & Newman 1999; Striedter 1999; Wagner 1999; Wilkins 2002); see Raff (1996) and Schlosser and Wagner (2004 and other chapters from the same book), for reviews and specific investigations on modularity or serial homology; (b) behavioural homology, which deals with the difficulties of defining behavioural characters, inferring behaviour from fossil evidence and with the great variability and propensity to experiential modification (Greene 1999; Proctor 1996); (c) research on genetic homology, in which (among others) the effect of gene duplication on homology (Holland & Garcia-Fernandez 1996; Holland 1999) and the evolutionary association and dissociation between genes and structures are investigated (Rosa-Molinar & Burke 2002; Wray 1999). As summarized by Hall (2013), genetic homology is applied to (a) genes that share nucleotide sequences (called orthology), (b) homologous sequences created by a gene duplication, that is related to another gene in the same genome (paralogy), (c) genes that share the same function; (d) genes with different functions, and/or similar networks (Hall 1994; Hall 1999, 335-352; Lauder 1994; Wagner 1999; Wake 1999; Wilkins 2002).

One of the most interesting developments in genetics is the discovery that homologous master genes can activate the development of structures traditionally regarded as non-homologous. For example, (as now well known) it was found that the independent evolution of eyes is due to the effect of master control genes or the so-called *Hox* gene system (Gehring 1996; Gehring 1997; Halder et al. 1995; Wilkins 2002, passim). In a classic review Salvini-Plawen and Mayr (1977) estimated that eyes or proto-eyes emerged independently 40 to 65 times in different phyletic groups or possibly even more. This example was often quoted to illustrate the power of selective pressure in the emergence of eyes in distantly related taxa (as in vertebrates, cephalopod molluscs and insects). This schema of convergent evolution cannot be entertained any longer, as it was based solely on the classical units of comparison in homology – morphology. The genetic data – more specifically the molecular conservation of the *pax-6* regulatory pathway – indicated that animal eyes evolved from one proto-eye (Arendt 2003; Tomarev 1997). However, the multiple origins of eyes still illustrate the power of natural selection when proposed in a more subtle schema: since the optic of the eyes from living organisms did not exist in the last common ancestor of these organisms, they were developed independently from a very simple photoreceptive spot.

Is it reasonable to use the term homology in connection with traits which are generated by different pathways? Butler and Saidel acknowledge this question, suggesting two new terms

in the field of comparative developmental biology: syngeny (or generative homology) and allogeny (or generative homoplasy). They formally define syngeny as “the relationship of a given character in different taxa that is produced by shared generative pathways” (Butler & Saidel 2000, 849); and allogeny as “the relationship of a given character in different pathways” (Butler & Saidel 2000, 849). It is possible that these terms will become useful or even indispensable in future discussions on homology. This terminology will not be used here, because the main focus of this work is on the use of convergence between distantly related species; nuances related to different levels of homology and parallelism in closely related species will only be relevant when the debate moves towards homology of behaviour.

The term “parallelism” is used to describe convergences within a set of species sharing several homologous structures, as instances of multiple and striking cases of convergences between marsupial and placental mammals. This term is strongly related to the German concept “*Homoiologie*” proposed by Ludwig Plate in early 1920’s to describe parallel traits which have a strong “homologous basis” – or in Plate’s (translated) words: traits which developed on the basis of the same structural conditions (Plate 1922, 475). *Homoiologie* refers to almost identical traits in closely related species which are exercising similar functions but which have been developed independently. An example of *Homoiologie* is the parallel evolution of eyestalks in several species of flies from the taxon Diptera (Hennig 1982, 117-118). The term *Homoiologie* was not first coined by Willi Hennig or by Rupert Riedl, as sometimes stated in the literature. Please note that the same term (homoiology) was also coined by Lieberman (1995) for homoplasies that are caused by nongenetic environmental factors. The term *Homoloilogie* in German is used here to differentiate from Liebermann’s homoiology.

It is not possible to distinguish unambiguously between convergent and parallel traits. For example, textbooks traditionally mention modern placental wolf (*Canis lupus*), the recently extinct marsupial Tasmanian wolf (*Thylacinus cynocephalus*) and the borhyaenid marsupial (*Prothylacynus patagonicus*) from the early Miocene period in southern Argentina (Bayrhuber et al. 1992, 451; see, e.g., Strickberger 2000, 457-458) as example for convergence *or* parallel evolution – depending from the author. The usual discussion on the possibility of a formal distinction between convergence and parallelism involves conflicting views of the role of natural selection and constraints in the evolution of traits (Arendt & Reznick 2008; Desutter-Grandcolas et al. 2005; Ghiselin 1976; Haas & Simpson 1946; Hall 2003; Hall 2007; Pearce 2012; Powell 2007; Stern 2013); for a discussion on the

terminological origin and debate about the meaning and utility of parallelism see Gould (2002, 1076-1088). As we will soon see, in this discussion it is sometimes ignored that the distinction between convergent and parallel traits is dependent on how the terms 'closely related' or 'distantly related organisms' are perceived by researchers working in different biological fields. The greatest possible generalisation refers to the fact that all earthly organisms descend from one or few forms and therefore, share the same basic characteristics – all earthly forms of life are dependent on nucleic acids, proteins and carbohydrates. From this particular point of view, all earthly organisms *are* closely related, as their similarity is established through a comparison with possible life forms beyond Earth. However, although this statement is important for discussions on astrobiology, it is of little practical value for biologists when discussing the different kind of non-homologous patterns of similarity between known living organisms; I will come back soon to the problem of distinguishing between parallel and convergent evolution.

In opposition to several biologists who consider it as important to differentiate between parallelism and convergence, cladists usually regard all cases of convergent traits, parallelism and reversals (= evolutionary reversion from a derived trait to an ancestral form) as noise in the data sets used to reconstruct phylogenies. For this reason, in cladistics there is the tendency to lump these concepts under the term "homoplasy" (Gr. *homós* same + *plassein* to mold). Although several pioneers of phylogenetic systematics used the term "convergence" for all similarities due to independent evolutionary changes (Ax 1984, 63; Hennig 1983, 9; Sudhaus & Rehfeld 1992, 111), modern cladists seem to see the term "homoplasy" as a less ambiguous term (see, e.g., Wiesemüller et al. 2003, 121). The terms "homoplasy" and "homogeny" were first proposed by E. Ray Lankester (1870): "homogeny" for homologous traits due to inheritance from a common ancestor, and "homoplasy" for similar traits resulting from independent evolution; in opposition to homoplasy, the term homogeny was never widely disseminated.

Similarly to the study of homology, there are several relevant aspects of homoplasy which can be discussed at various levels of biological organization (Armbruster 1996; Brooks 1996; Doyle 1996; Foster et al. 1996; Hufford 1996; McShea 1996; Sanderson & Hufford 1996; Wake 1996). One is the relationship between homology and parallelism and convergence. As a short review of the earlier literature shows, this discussion did not start through new data on master genes – the genetic insights of the last 25 years only gave new input to the debate. Kosswig (1961), for instance, pointed out that similar (homologous) features do not have to

rely on the same genes and that typical parallel structures or convergences also do not have to rely on the same genes; he defended parallelism and convergence as part of a continuum. Starck (1978, 14) distinguished convergence from parallelism, but recognized that it is sometimes difficult to distinguish them. Remane (1961, 459) stated that an attempt to make a sharp distinction between convergence and parallelism is not productive. According to Simpson (1972, 127), the delimitation between convergence and parallelism is unclear. He pointed out that, although there are not clear boundaries between parallelism and convergences, in most clear cases we can observe that convergence increases the degree of similarity between organisms, which is not true for parallelism. This view is similar to the ideas proposed by Haas and Simpson (1946). In a classical paper, they reviewed several terms (homology, homogeny, analogy, homoplasy, divergence, parallelism, convergence, homeomorphy, mimicry, etc.). They referred to the topic parallelism/convergence as follows: "Other special cases of homoplasy are convergence and parallelism, distinction between which should be based on whether or not similarity increases with evolution rather than on degree of relationship between the lines involved" (1946, 344).

In a review of the relationship between parallelism and convergence, Hall (2003) compared features classified as homologous with features normally identified as homoplastic, and aligned the following terms as part of a continuum: homology → reversals → rudiments → vestiges → atavisms → parallelism, and classified convergence as the only class of homoplasy (Hall 2003). The view of convergence as its own class is basically the same as proposed by Lankester (1870), which was explicitly acknowledged by Hall; see also similar opinions by other authors (Hodin 2000; Sluys 1989). Hall's view of parallelisms as features "present in lineages but not in their most recent common ancestors (otherwise homology), as similar genetic and developmental mechanisms in different lineages respond to influences (external or mutational) by producing similar features" (Hall 2003, 411) is classical, and may still be popular in modern biology.

It is difficult to accept Hall's rather unusual views on an absolute distinction between parallelism and convergence. Also uncommon is his absolute denial of the parallelism phenomenon, as defended by Arendt and Reznick (2008). They argue that there is no distinction between convergence and parallelism, since there might be convergences in closely related species by mutations in different genes or convergent in distantly related species by mutations in the same genes. They regard the terms convergence and parallelism as a relic of a time when the underlying causes of phenotypic similarity were not well

understood and were confined to inferences based on comparative anatomy. They suggest only using the term convergence and dropping the term parallelism.

This specific discussion reveals how often attempts to define terms that describe complex biological phenomena imply oversimplifications, dichotomies, and a readiness to accept tautological elements. The classical view is probably still the best: convergences and parallelism are regarded as expressing real biological phenomena, but a sharp distinction is not always possible. For instance, as stated above, the term "parallelism" is used to describe the multiple and striking cases of (convergent? parallel?) non-homologous traits between marsupial and placental mammals. It is virtually impossible to distinguish those cases where convergence emerged by different evolutionary pathways, from the cases of homoplasy that might occur when closely related species react similarly, but by different developmental pathways to similar selective pressures.

It is argued here that these hypothetical "pseudo-parallelisms" can hardly be distinguished from parallelism that emerged through channelled developments. The decision to term these cases "parallelism" or "convergence" depends on subjective criteria, and it is possible that the discussion on convergence / parallelism will ever come to definitive agreement. The same author even defines in some publications convergence as basically distinct from parallelism and in other publications argues that there is no fundamental difference between both phenomena; Hall (2003, 420) pointed out such a contradiction in the works by G. G. Simpson. I tend to agree with biologists who find it feasible to distinguish in some cases between convergence and parallelism, like Leander, who argues as follows:

> *When considering lineages with phylogenetic distances that are much greater than those found in vertebrates, and animals as a whole, there are many examples of evolutionary convergence that are not constrained by homologous developmental networks. These examples reflect ultimate convergence and more proximate cases of convergence – parallel evolution – is appropriate and informative, if for no other reason than to help guide future research on the genetics of adaptation.* (Leander 2008, 482)

For the present thesis, the most relevant cases of convergence are those based definitively on different developmental mechanisms – the impressive similarity between hummingbirds (Trochilidae) and the hummingbird hawk moth (*Macroglossum stellatarum*) is an example which is not controversial; cases in which an "ancestral" developmental mechanism or regulatory genes reappeared will not be considered in the guidelines of the here proposed convergence approach, which deals basically with distantly related species.

Another terminological issue concerns the attempts to distinguish unambiguously between "analogue" and "convergent" traits (Homberger 2001; Remane et al. 1972, 238). As representative of this view, Remane, Storch and Welsch (1972, 238) termed the similarity between organs which are not homologous as "analogue", for example, wings from insects and vertebrates; the similarity built from organs which are homolog are called "*homoiolog"*, for example, wings from bats and pterosaurs; finally they used the term "convergent" for similarities which emerged from completely different basic organs (*Grundorgane*), like the medusa-like form in Protozoa (*Craspedotella*) and Cnidaria. We have seen above the problems with the term *Homoiologie* (which implies a distinction between convergence and parallelism). We find similar problems with the differentiation between analogy and convergence. For example, how reliable is the statement that bats, pterosaurs and birds have wings emerging from "homologous" organs? The answer is positive when considering the forelimb and assuming a high degree of oversimplification; the answer is negative if we consider more carefully details of the structures, for instance, the material used to enlarge the paired surfaces used to fly – stiff feathers in birds, skin in bats and pterosaurs. Here we could assume – also implying oversimplifications concerning the anatomy of the wings (Wellnhofer 1993, 46) – that pterosaurs are "closer" to bats than pterosaurs and bats to birds, which would also change the terminology suggested by Remane, Storch and Welsch above. For this reason, the terms "convergent" and "analogue" are here used as synonymous when treating organismic features. Unfortunately, the use of the same term (analogy) in the sense of "analogical reasoning" (see above) and in the sense used in biology can lead to confusion. We use "analogical reasoning" in the process to identify possible "analogies" (convergences). This double use of this term is related to historical facts, and the term analogy has a long tradition of being used as synonymous to convergence and can for this reason not be simply dropped from the vocabulary. See for instance, the expression *Analogienforschung* ("analogy research") used by Hans Böker (1935, 4) and *Analogienbiologie* (analogy biology) used by Hans-Wilhelm Koepcke (1971, 195).

2.3 Adaptation and adaptive analyses: some basic concepts

In 18th and early 19th century, the concept of a match between organismic traits and their environment became an intrinsic part of (mainly non-evolutionary) natural science, as for example in natural theology (Amundson 1996; Lauder 1996; Ospovat 1978). Like the ideas expressed in natural theology, the evolutionary thoughts expressed in pre-Darwinian times (see Appendix B) were not characterized by sophisticated discussion on adaptation.

After 1859, the topic "adaptation" has been treated in an impressive number of works and the range of relevant opinions expressed on this subject cannot be covered here. Instead, in the present section I will point out some aspects of the discussion which are relevant to the use of convergence as a tool and for the topic "water use in primates". This approach is reflected in the examples used in the text, which often refer to the topic swimming and diving in terrestrial organisms.

A remark is needed here about the use of the word "adaptation" in physiology. In opposition to evolutionary biology, in several works on physiology the term adaptation refers to a broad range of short-term physiological responses to non-lethal levels of an environmental stimulus (see Bennett 1997), for instance (a) cardiovascular responses observed in humans when they immerse the whole body or parts of the body in cold water (Andersson *et al*. 2000), (b) the changes in temperature tolerance observed when animals experience climatic changes (called "acclimatization" under natural conditions, and "acclimation", under experimental conditions) (Schmidt-Nielsen 1975, 283-295); (c) the mechanisms of accommodations observed in vertebrate eyes when they change optical power to maintain a clear focus on an object, as this object changes its distance to the eyes (Neuweiler 2003, passim). The term "adaptation" as used in physiological literature is definitively not synonymous to the term adaptations used in evolutionary biology – the ability to acclimatize is the *product* of an evolutionary process. One would expect that the differences between short-term physiological adaptations and evolutionary adaptations (see below) can usually be distinguished from the context in which these ideas are expressed. It seems, though, that especially in physiological publications the distinction is not always clear.[11]

In modern evolutionary biology, the term adaptation has different meanings. As pointed out by Munson (1971), adaptation is used to denote (1) traits; to denote (2) an organism or species which is in a certain state; to refer to (3) the state itself; to refer to (4) the process of which the state is an outcome. Although the distinction between these different uses is often

[11] Chauncey D. Leake (1964) discusses the historical background of the term adaptation in an introductory chapter of the book *Adaptation to the Environment*, section 4 of *Handbook of Physiology.* He smoothly passes from an analysis of early concepts of *physiological adaptations* to a discussion on the emergence of the *evolutionary concept of adaptation* (referring to, Lamarck, Darwin and Wallace), and back to an analysis of investigations on *physiological adaptations* from the 19th century. By using the same term (adaptation) without definition at any point of his article, he does not allow the reader to differentiate between the different concepts. An example of clear distinction of the terms is supplied by Albert F. Bennett (1997), who wrote a book chapter on adaptation in issue 13 of the same work (*Handbook of Physiology*). The differences between both authors are probably related to their different intellectual backgrounds: Leake was trained as a pharmacologist and medical historian; Bennett is a zoologist, whose main research interests are evolutionary and comparative physiology.

acknowledged in reviews on the topic adaptation it has been pointed out that these terms are often conflated in discussions of adaptation (Gould & Vrba 1982). On the other hand, Ross and Lockwood pointed out that "It seems reasonable to require that these uses apply definitions that are compatible, or at least not contradictory" (Ross & Lockwood 2002, 2); see also Stern (1970). Although context alone might prevent confusion in several cases, confusion can be also avoided with some simple procedures, as proposed by Munson. After he presented a list of the multiplicity of use of the word adaptation (see above), he argued that "there is no need to use the same term in every kind of cases" (Munson 1971, 201) –, offering the following suggestions:

> To avoid the indeterminacy, I shall usually, though not always, use the phrase "adaptive trait" rather than "an adaptation". I shall never speak of an organism or species as being a case of adaptation. For this and for "the adaptation" (i.e. the state), I shall speak only of an adapted organism or species. The only use of "adaptation" as verb form is (4) [see above]. Since the process takes its name from its outcome, it only generates confusion to refer to both the state and the process by the same term. Accordingly, I here shall not refer to the changes and procedures by which an organism becomes adapted as "adaptation". Whatever those processes may be, they will simply be designated in some other way. In sum, "adaptation" (except in straight-forward contexts) will be used only in the phrase "an adaptation", and this is always to be read as referring to a trait which is asserted to be adaptive. (Munson 1971, 201)

Munson's advice will also be considered in the present work; the main deviance of this suggestion refers to the here suggested term "functional focus", defined in chapter 3.2.

One of the most common definitions of adaptation in modern biology contains three pre-conditions: adaptation is a trait that (1) enhances fitness or performance; (2) is fixed in a population by natural selection (3) to perform current function (Coddington 1988; Gould & Vrba 1982; Lauder 1996). Point (1) is accepted by most workers; divergences are common concerning points (2) and (3). Strictly speaking, the definition above implies that a researcher can only refer to a trait as an adaptation, if a clear picture of the evolutionary events leading to the specific trait is known. (The opposite is also true: statements on a trait as being "something else" than an adaptation imply precise information on how this trait evolved, which functions it performed or did not perform in the past and which functional changes occurred during the evolution of this trait.)

Some researchers assume, therefore, that it is not important to know how a trait emerged in the evolutionary process; most works quoted in this context are those published by Walter J.

Bock and Gerd von Wahlert (Bock 1967; Bock 1980; Bock 1989; Bock & Wahlert 1965); more recent publications usually connected to these ideas are those by (Fisher 1985; Kay & Cartmill 1977; Reeve & Sherman 1993). Although most of these proponents of what is sometimes called a non-historical concept of adaptation (Lauder 1996; reviewed by Ross & Lockwood 2002) usually assume that adaptations emerged and are maintained by natural selection, they tend to regard it as unnecessary to identify selection forces in the evolution of traits; consequently, they usually define adaptation as traits that increase the fitness of an organism.

Part of the divergent views on adaptation is that some researchers acknowledge the difficulty of reconstructing the historical pathways of traits. According to this view – as explained by Gould and Vrba (1982), some researchers "prefer Bock's broad definition, because it is more easily operational. We can observe and experiment to determine what good a feature does for an organism now" (Gould & Vrba 1982, 7).

The conflict and misconceptions related to different or imprecise terminology motivated Gould and Vrba (1982) to propose new terms to improve the discussion on adaptation. Referring explicitly to the views expressed by George C. Williams in his influential work *Adaptation and Natural Selection* (1966), they reinforced William's definition of adaptation as traits shaped by natural selection for a current use. They also follow Williams in labelling the operation of a useful character, not built by selection for its current role, as an "effect"; however, they see the need for a term to designate unselected, but useful characters. They suggest for such traits the term "exaptation" – a term once often labelled as "preadaptation". According to Gould and Vrba, exaptation can be "A character, previously shaped by natural selection for a particular function" and coopted [= exapted] for a new use" or "A character whose origin cannot be ascribed to the direct action of natural selection (a nonadaptation)" and coopted for current use (Gould & Vrba 1982, 5). They explained that they "are not trying to dismantle Bock's concept. We merely argue that it should be called aptation (with adaptation and exaptation as its modes). As aptation, it retains all the favorable properties for testing enumerated above" (Gould & Vrba 1982, 7).

The fact that Gould and Vrba's terminology is discussed by several reviewers of the topic adaptation reveals the importance of the term exaptation. Nonetheless, this terminology was not adopted by several biologists (Alexander 1998; Dennett 1998) and has not led to a consensus among biologists concerning the best terminology to be used in practical research. One of the primary points of the discussion is related to the practical difficulty in

distinguishing between adaptation and exaptation. This view is expressed in following statement by Ross and Lockwood:

> We appreciate the logical rigor of the historical definition of adaptation because it is intimately tied to the theory of natural selection, and adaptation is the phenomenon that natural selection sets out to explain (Darwin, 1859). However, because it is impossible to demonstrate that selection was involved in the fixation of most traits, accepting the historical definition forces one to accept the definitive identification of adaptations is impossible in most cases (Williams, 1966: 4; Ross, 1999). This in turn implies that when studying fossil taxa, although one can study morphology and try to reconstruct behavior and function, one cannot prove or disprove a hypothesis of adaptation without making some significant assumptions about trait heritability, population structure, and past selective regimes.(Ross & Lockwood 2002, 3)

And later in the same paper:

> [...] historical definitions that link adaptation to natural selection are true to evolutionary theory. Unfortunately they are virtually impossible to apply, particularly to the fossil record. Thus, while the historical definition discussed above is most accurate in theory, it is almost useless in practice. The most productive approach to date has been the nonhistorical approach. Less concerned with trait origination, this approach has arguably more realistic goals: the reconstruction of behavior for its own sake. (Ross & Lockwood 2002, 34)

In their analysis of the comparative method, Leroi, Rose and Lauder expressed their scepticism of the usefulness of the terms proposed by Gould and Vrba:

> Unlike Gould and Lewontin (1979), we do not hypothesize that many traits are not adaptive. Rather, we are making the case that the adaptive (or not adaptive) nature of traits cannot be determined from most comparative data. If, as we suggest, historical study of the evolutionary process is subject to strict limitations, then the various terms proposed to describe such processes or characters are also subject to greatly restricted use. These include the terms adaptation, exaptation, disaptation, or aptation (Gould and Vrba 1982; Baum and Larson 1991), all of which imply direct and specific knowledge of selection forces in the past and the pattern of genetic correlation among these characters. (Leroi et al. 1994, 397-398)

We will return later to this conflict between the logical rigour of Gould and Vrba's terms and the need for a terminology to be used in practical research on adaptation.

2.4 On the dichotomy between research focusing on homology and convergence

Textbooks usually refer to convergences in two senses: first to show that homoplastic traits can be deceptive, since they cannot reliably indicate phylogenetic relationships; second to illustrate the power of natural selection to produce non-homologous patterns of similarities. In early and modern publications it is also often assumed that the study of adaptive traits through the use of convergences and homologies are competitive methods. Although it is understandable that scientists often use dichotomies to stress aspects of their own research, this polarization often implies an oversimplification. Generally speaking, dichotomies reflect the need in science to treat a certain aspect of a discussion in opposition and distinction to others.[12] These polarizations are necessary and useful when the discussion is based on a real dichotomy. However, when pointing to dichotomies, it is important to consider the nuances which contradict or weaken the establishment of polarized views and this applies also to the discussion "convergence versus homology" in the investigation of adaptations. Formal methods aiming at identifying and removing convergences from systematics are certainly more widespread than the use of convergent patterns in the evaluation of adaptations. Although several investigations were carried out on the history and research of homology, the present work supplies (to my knowledge) the first attempt to review the use of convergence as a tool in natural sciences. This indicates clearly that the most evident and acknowledged perspective used by biologists is of "convergence as a noise" and not the perspective of "convergence as a tool" (Bender 1999; Scott 1891, 369; Wiens et al. 2003).

However, both homology *and*[13] convergence are implied in practically *all* thoughts on adaptation, even though investigators are not always aware on this. The human ability to recognize patterns of similarities in organismic features that emerged through common ancestry is not only the product of rational methods developed by scientists, but observable in all human cultures (Atran 1993; 2013; Berlin 1973; Berlin 1992). As stated by Hall "Consciously or unconsciously, we invoke homology whenever we compare two or more

[12] For interesting thoughts concerning our need to see a system in opposition and distinction to others see Haggett and Chorley (1969). On misleading or false dichotomies in science see also Gould (1987, 8-10) and Cosmides and Tooby (1994); on the problems related to oversimplifications in science see Bunge (1963). For other discussions on the topic "simplicity" in scientific theories (especially related to methodological falsificationism) see Lakatos (2001, passim); for a very useful discussion on philosophy of science in which among others the theories of Karl Popper, Imre Lakatos, Thomas Kuhn, and Paul Feyerabend are summarized and critically reviewed see Chalmers (1992).

[13] I regard the use of convergence as a tool and the study of homologies not as competitive, but as complementary approaches. The same idea was expressed by Wolfgang Wickler in a popular book on ethology (Wickler 1971a). Like several other ethologists, Wickler regularly expressed thoughts on adaptations from the point of view of convergence; see, e.g., Wickler (1971b; 1972).

biological units, whether those units are genes, cells, tissues, organs, structures, behaviour or individuals" (Hall 2003, 410). As shown elsewhere (Appendix A and B), humans have also the ability to recognize patterns of similarity which did not arise through common ancestry, since they are the product of similar selective pressure in independent lineages. Regardless of which method individual researchers apply for their analyses of adaptations, previous knowledge on adaptive features found in living organisms (expressed, for example, in convergent features of traits related to flying, digging and burrowing, hunting, swimming, concealing, thermoregulation, and many others) will always play a crucial role at different levels of research. This knowledge – even if sometimes only unconsciously present – is fundamental in our assumptions on anatomical traits and behaviours performing a certain biological role when interacting with a certain spectrum of the environment. We "know" that "wings" are used for flying, because we can observe daily several and distantly related organisms with wing-like structures (developed independently from each other) which are obviously used for this specific locomotion; we also observe that organisms from the same taxa without wings are not able to fly. Based on these trivial, but important observations, we can infer that extinct organisms with wing-like structures like *Pterodactylus* (as pointed out by Cuvier, see below, chapter 2.5.3) were probably using such structures to fly. The opposite is also true. Following a similar logic, we do not know exactly how saber-tooth cats (some Felidae and most Nimravidae) used their oversized upper canines, as we cannot observe living analogues to the extinct saber-tooth cats. Although several hypotheses were proposed to explain the function of canine teeth (some authors even arguing that these traits did not evolve by natural selection), most specialists agreed that these traits evolved convergently in four different groups of animals. This speaks to the idea that the long canines were successful adaptations and most authors agree that they were used for killing prey; several hypotheses were proposed to explain exactly how the canines were used (Akersten 1985; Antón et al. 1998; Antón & Galobart 1999; Emerson & Radinsky 1980; Simpson 1941). Some researchers follow another approach. Instead of focusing on the large upper canines and their associated modifications – which have been central in most functional studies on saber-tooth cats – they are interested in other aspects of the anatomy of saber-toothed carnivorans which are consistently different from other carnivorans, for example, the carnassials of saber-tooth cats. As explained by Bryant and Russell, the carnassials of saber-toothed cats "are placed more posteriorly, and experienced higher rates of attritional wear than those of most other carnivorans. The correlation of these attributes with the sabertooth morphotype suggests some functional association" (Bryant & Russell 1997, 116). As we will see, the use of different

perspectives and approaches in functional analyses is important for the formulation of hypotheses concerning the evolution of traits.

In the following section we will see that the use of convergence is very widespread in biology, although some uses of analogy are only implicit in biological publications (see also Appendix A and B on the role of analogies in early natural sciences).

2.5 The use of convergence in the formulation of hypotheses on adaptation

2.5.1 Overview of works/disciplines/concepts using convergence as a source of knowledge in biology

In the early 20th century, many biologists from different disciplines tried to integrate concepts based on convergent evolution in their investigations, using different backgrounds. Space limitation makes it impossible to review in details these ideas; the following review is only an overview of the works that I know and regard as important in this context. Beside the works quoted in the introduction of this thesis, important contributions can be found in D'Arcy Thompson's seminal work *On Growth and Form* on morphogenesis (Thompson 1942 (first publ. 1917)), in Othenio Abel's methods of palaeobiological research (1912; 1931a), in Hans Böker's "biological anatomy" (*biologische Anatomie*) (1935; 1937); and in the works by Michael Nowikoff (1930) and Arthur Willey (1911). Convergence and parallel evolution were also important in some early ethological works (Espinas 1878; Petrucci 1905; 1906; Rabaud 1925; Waxweiler 1906); most of them rather ignored today. The term "convergence approach" (German: *Konvergenzforschung*) was used independently by different authors with quite different meanings, as for instance in connection with the use of analogies in hypotheses on early hominin evolution (Bender 1999), in ethological investigations (Wickler 1971a) and as a complementary method to the investigation of homologies (Coddington 1994). Convergence is also essential in the "likelihood approach" for the analysis of adaptation (Baum & Donoghue 2001), and in several comparative approaches in morphology and physiology (Schwenk 2000b, and references therein).

Non-homologous patterns of similarity were used for the formulation of useful generalizations of biological phenomena, as for instance in (a) the description of patterns of territoriality in birds by Henry Eliot Howard (1920); in (b) hypotheses focusing on certain aspects of ontogenetic development, as for instance the division between *Nesthocker* (nest-squaters, or nidicolous) and *Nestflüchter* (nest-fleers, or nidifugous) proposed by Lorenz

Oken (1837, 24, 380) and in (c) the terms “altricial” and “precocial” organisms proposed by Carl Jakob Sundeval (see Starck & Ricklefs 1998; 1836).

Explicit arguments for the use of convergences as an analytical tool in evaluating design were expressed by influential authors like Konrad Lorenz in his paper *Analogy as a source of knowledge* (Lorenz 1974) and by Stephen J. Gould in his paper *In defense of the analog: a commentary to N. Hotton* (Gould 1976). Kurt Schwenk expressed the value of analogies in the examination of the “evolutionary dynamic between extrinsic factors (e.g., environmental selection, adaptation) and intrinsic factors (e.g., developmental and functional constraint) in determining form” (2000b, 4). The comparison between distantly related species was often useful to show the different resources used by organisms to achieve the same end results (Maina 1998). The terms “r-selection” and “K-selection” coined by Robert MacArthur and Edward O. Wilson (1969) is also applicable for distantly related species. Convergences can be used also to predict adaptive patterns, in a few cases with surprising results in practice. For instance, Alexander’s speculations on a theoretical mammal developing eusociality similar to social insects led to the ‘discovery’ of such adaptations in the African naked mole-rat (*Heterocephalus glaber*) (Alexander et al. 1991).

Convergence as a tool in the analyses of adaptive features is sometimes explicitly (but often only implicitly) used in several biological disciplines, as for instance in (a) the integrative field of ecomorphology (Bock 1994; Garland, Jr. & Losos 1994; Losos 2011; Losos & Miles 1994; Reilly & Wainright 1994; Wainright 1994); (b) regressive evolution (Schemmel 1984); (c) the study of fossorial organisms, or proficient burrowers (Böker 1935; Nevo 1999; Rose & Emry 1983; Rose & Koenigswald 2005; Starck 1961); (d) botany (Fenner & Thomson 2005); (e) cryobiology (Muldrew et al. 2004; Storey & Storey 2004); (f) ornithology (Cody 1969; 1973a; 1973b; Trewick 1997); (g) comparative physiology (Heinrich 1999; Heldmaier 2003; Neuweiler 2003; Schmidt-Nielsen 1964; Vague & Fenasse 1965); (h) comparative brain anatomy and physiology (Manger 2006); (i) all disciplines working synergistically on the inference of function in fossil structure, for example, vertebrate in invertebrate locomotion, biomechanics and palaeobiology;[14] (j) bionics (Hill 2001; Nachtigall 1974); (k) insect

[14] I doubt that the identification of an adaptive trait in fossil organisms which is divergent from the traits found in living closely related species can be inferred without the use of comparisons with potential convergent traits of living organisms. The following references are only a few of the works published on this topic (Abel 1912; 1914; 1925; 1929; 1931a; Alexander 1983b; Böker 1935; Bonner & Horn 2000 and other chapters in the same book; Carroll 1997; Etter 1994; Hickman 1988; Kay 1975; Kay & Covert 1984; Koenigswald et al. 2005; Lugar 1990; Niethammer 1979; O'Leary & Rose 1995; Rayner 1981; Rose & Emry 1993; Rudwick 1964; Schmidt-Nielsen 1985; Seilacher 1974; Slijper 1946; Taylor et al. 1970; Vogel 1998a; 2001; 2006); see Appendix C for

polymorphism (Leuckart 1851; Schmidt 1987) and other aspects of entomology (Eidmann & Kühlhorn 1970; Weber 1954); (l) palaeobiogeographical inference and interpretation (Ball 1975; Newton 1990); (m) in several attempts to classify organisms according to functional features (see Appendix C for explanations and references);[15] (n) ethology (Bender-Oser 2006; Bshary et al. 2007; Fagen 1981; Hansell 2005; Kamil 1998; Shettleworth & Hampton 1998; Shumaker et al. 2011; Taborsky 2001; Vander Wall 1990; Wickler 1971a) and (o) methods used to investigate adaptive traits focusing on comparative analyses of closely related species, often labelled 'comparative method' or 'phylogenetic comparative method'.

It is difficult to give a specific definition of the phylogenetic comparative method due to the high diversity of approaches used by single investigators (Harvey & Pagel 1991; Kamil 1998; Krebs & Davies 1993: 24-47; Lack 1947; Larson & Losos 1996; Martins 2000; Martins & Housworth 2002; Pagel & Harvey 1988; Ridley 1983; Tinbergen 1953). Instead of a definition, a general description of what is regarded as the main characteristic of this approach is probably more useful, as for instance following by Harvey and Pagel:

> The major advance has been the development of methods based on explicit evolutionary and statistical methods. These techniques take careful stock of the phylogenetic links between species, and marry ideas about evolutionary changes with statistical processes in such a way that formal tests of hypotheses about the evolution are possible. (Harvey & Pagel 1991, 2)

It seems that the emergence of the phylogenetic comparative method is connected to three phenomena: firstly, to the increasing use of computer analyses in systematics; secondly to the dominant role that cladistics played in systematics from the end of the 1980s onwards; and thirdly to the counter-movement following the criticism towards analyses of adaptations by George C. Williams (1966) and especially by Stephen J. Gould and Richard Lewontin (1979). Through this criticism, the terms "adaptationism" and "adaptation" became pejoratives

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earlier publications and below for further modern references on the use of convergent traits in the interpretation of fossil evidence.

[15] Some attempts to classify plants according to plant function in the ecosystem are known by the term "growth-forms" or "life-forms". One publication on life-forms in zoology deserves a special mention: Hans-Wilhelm Koepcke's attempt to make the ecological aspects of biological research axiomatic (Koepcke 1971; 1973). Working with the concept of life forms, he was mainly interested in how species could be classified by non-phylogenetic systematics based on clear adaptive features of living organisms. I consider his work of great importance, both because of his ambitious and visionary attempt to formulate a method to classify all life forms, as well as for the astonishing amount of material he collected to corroborate his ideas. On the other hand, the main problem of this investigation is related to the readiness in which Koepcke accepted several superficial non-homologous patterns of similarity as adaptive. Most important for the present study is that Koepcke did not investigate the use of convergences in the evaluation of complex features in extinct or extant species, or in the evaluation of a feature concerning its status as "adaptive" or "non-adaptive". His main concern was to build up a system to allow him to discuss exobiological topics.

(Amundson 1996; see Rose & Lauder 1996). Therefore, the phylogenetic comparative method was implicitly seen by some biologists as an answer to the need of more rigorous methods in the analyses of adaptations.

However, these methods have also limitations. For instance, hypotheses on the emergence of organismic traits are highly dependent from the accuracy of cladistic analyses used in single studies. As emphasized by Harvey and Pagel, comparative biologists "are never sure that we have the correct tree. Comparative biologists should be aware of the fact that they may well be working with the wrong tree!" (Harvey & Pagel 1991, 70-71). This limitation is sometimes used as an argument against the use of comparative methods (Reeve & Sherman 1993). However, Baum and Donoghue regarded this criticism as unjustified "because any scientific inference will fail if the underlying assumptions are not met" (Baum & Donoghue 2001, 26). Another criticism to the comparative method was expressed by Leroi, Rose and Lauder. They argued that "knowledge of the phylogenetic distribution of traits, their performance, and selective regimes are not sufficient to identify adaptations" (Leroi *et al.* 1994, 383). According to them, in the absence of information on the relative fitness of a putative adaptation and the trait it supplants, as well as genetic data, "phylogenetic patterns will often suggest that a trait is an adaptation when in fact it is not and suggest that it is not, when in fact it is" (Leroi *et al.* 1994, 383); they concluded: "We do recognize the rather severe limitations that our prescriptions place on retrospective studies of adaptation and evolutionary constraint. But we consider that such limitations are better seen clearly than obscured by false hopes about the ability of comparative studies to resolve the processes of evolution" (Leroi *et al.* 1994, 398).

A further restriction of the method is that widespread taxa cannot be accommodated in the cladistic approach, what excludes the possibility to compare non-homologous patterns of similarity between, for instance, distantly related marine reptiles (Lindgren *et al.* 2014), large mammalian clawed herbivores (Coombs 1983) or 'thunniform' body shapes in several different groups of animals (Bernal *et al.* 2001; Donley *et al.* 2004).

There are several other lines of evidence on the use of convergences in functional analyses. The interpretation of functional morphology in extant organisms is mainly based on observation of how organisms live and how they use certain traits in their interaction with the environment; some of these hypotheses can be tested in experiments (Cowen 1979). The functional morphology of extinct organisms is more complex, since only certain aspects of

their anatomy and behaviour can be inferred from fossils. However, as Hickman aptly stated, the dichotomy extant organism /extinct organism is not very clear:

> In fact, much of what we think we know about the function of living organisms is derived from the data of routine systematics and static images of form. Imaging processes, like the fossilization process, filter the information that we retrieve about form. And some of what we think we know about the function of fossil organisms is derived from simple experiments. The problem of knowing a living organism and the problem of knowing a fossil organism are not really so different in the sense that both must proceed from some level of understanding of form itself. (Hickman 1988, 775)

The reconstruction of behaviours, structures, and ecology of extinct organisms are intrinsically related – structures are linked to function and organisms use their structures to interact with their environment. Knowledge of the form/function relationship in extant organisms is used to understand the functionality of structures from other extant organisms. On the other hand, knowledge of extant organisms helps us to understand the function of extinct organisms' structures which are known only from fossil record or from structures which are not fossilized, like soft tissue.

Space limitations prevent a detailed treatment of concepts used in the inferences of functions of structures of extinct organisms. Several authors summarize the main methodological concepts used in functional morphology; see, e.g., Briggs (2005), Etter (1994, 15-47), Lugar (1990), Prothero (2013) and Lauder (1997 and other chapters of the book). In the field of theoretical morphology and in Rudwick's paradigm method (see below in this chapter), invertebrates play a crucial role. For theoretical morphology reviews see McGhee (2007; 2009). McGhee explains the concept of theoretical morphospaces and the use of mathematical simulation of form, with a comprehensive list of references on the subject; see also Hickman (1993). Specific works on the methods used for the reconstruction of behavioural and morphological adaptations in primates were published by several authors (Chivers et al. 1984; Jungers & Godfrey 2002; Kay 1977; Kay 1975; Kay & Covert 1984; Kay & Williams 2002; Nunn 2002; Plavcan 2002; Plavcan & Kay 2002; Red 2002; Rose 1984; Ross & Lockwood 2002). Very useful are the works by Kay and Cartmill (1977) and Kay and Covert (1984), where theoretical aspects of functional analyses of extinct primates are discussed and operational rules for assessing adaptation are formulated.

Influential ideas on the use of analogy as a source of insight into the function of extinct organisms – especially in the investigation of invertebrates – were expressed by Martin

Rudwick (1961). He was intrigued by the cone-shaped Permian brachiopods known as the richthofeniaceans. He hypothesized that the lid-like brachial valve placed in the open mouth of the cone-shaped pedicle valves (which apparently could seal off this opening) was able to move rapidly, creating eddies that would swirled in and out the conical ventral valve. In Rudwick's hypothesis, richthofeniaceans were not feeding by ciliary action, as common in most brachiopods, but by this rhythmic flow mechanism. Rudwick demonstrated that many of the anomalous morphological traits of the richthofeniaceans could be explained as intrinsic parts of this feeding mechanism. Later, Rudwick (1964) proposed the "paradigm method" aiming at a formalized concept for the interpretation of fossil evidence where closely related species were not helpful and analogies with distantly related species not easily recognized. The paradigm method is a functional analysis of traits using a thought experiment. An organism is placed into an idealized configuration – the paradigm - and hypotheses are formulated on the function of traits to perform maximal efficiency under the limitation imposed by the nature of the materials. The method can be used to test predictions and reject models which are less efficient. Lugar aptly summarized the essential aspects and advantages of Rudwick's method:

> The paradigm method is most useful when several functional hypotheses are being tested. Thus the application of the method proceeds by postulating several functions for a structure, specifying an optimally efficient form for each function, and examining the degree of resemblance the form possessed by the organism and those postulated by the researcher. The paradigmatic form with the closest fit to the real form may be judged to represent the actual function of the structure. The ideal forms that serve as the source of the analogy are usually chosen from classes of machine, such as pumps, levers, or bridges, for which mechanical engineering can be used to specify the optimal design for accomplishing a specific task. (Lugar 1990, 310)

Although some authors criticized the paradigm method (Gould & Lewontin 1979; e.g., Grant 1975; Signor 1982), Rudwick's concept can probably be considered as the standard formal approach to the use of analogies with machines.[16] Cowen wrote a paper with Rudwick on the functional morphology of some aberrant strophomenide brachiopods from the Permian of Sicily. In this paper they proposed a tidal-flow feeding mechanism (instead of the usual ciliary feeding system) also for the lyttoniacean morphology, envisaging a more gentle movement of the dorsal valve in this group compared to the richthofeniacean (Rudwick &

[16] An often quoted work on the paradigm method is (Fisher 1985), in which Rudwick's concept is translated into a problem of Bayesian inference; see also (Cowen 1975, 24), who defends Rudwick's functional interpretation of flapping valves in brachiopods.

Cowen 1968). When Cowen defended the concept of flapping valves in brachiopods against the criticism by Grant, he argued that there is "often little conceptual difficulty" in using morphological analysis and analogy with "any available living group" when no living representatives of a group are available (Cowen 1975, 24). He aptly argued that the existence of living representatives might even limit the variety of analogues to be used in the interpretation of fossils. He illustrated this point with following examples:

> The reconstructions of dinosaur paleobiology by Ostrom, Bakker and others have met severe criticism, mainly because large living savanna mammals rather than living reptiles were used as appropriate analogues. In fact, the use of homology in functional reconstruction is only as good as the similarity of biological function of the structures being compared; thus while homological comparisons are usually superior to others, they are not universally so. In the case of the Permian richthofeniacean and lyttoniacean brachiopods, Rudwick's interpretation relies on analogies outside the brachiopods rather than homologies within the phylum. (Cowen 1975, 24)

Kay and Cartmill, by succinctly mentioning the use of analogies in their criteria for functional analyses in extinct species assumed that there must be some living species which have the morphological trait of the extinct species, otherwise no analogy would be possible (Kay & Cartmill 1977). The problem is that the use of analogies as expressed by Cowen and by Kay and Cartmill also has to be part of a convergence approach. I think that several problems in the contextualization of early hominins (see Appendix D and chapter 6) arise from the lack of such an approach.

2.5.2 Problems related to comparisons of non-homologous patterns of similarity between distantly related species

The identification of convergences between distantly related organisms is usually not established through a formal methodology for three main reasons: humans are able to recognize clear functional relationships (e.g., wings used to fly) and to recognize convergent patterns in organisms (wings in distantly related species). This process occurs not as an output of extensive scientific investigations, but "intuitively", often after an immediate encounter with an object. A countless number of convergences are not only easily detectable - they are eye-catching and sometimes misleading in relation to an initial subjective classification of the observed organism. For instance, ornithologists from the Swiss Ornithological Institute sporadically receive calls and emails with attached photos from people who believed that they saw a "baby hummingbird" in their gardens (Roman Graf, personal communication). In most cases they usually saw a hummingbird hawk-moth (*Macroglossum stellatarum*), a typical

example of convergence between birds and insects. The identification of the convergence takes place through the optic perception of the typical flying behaviour (hovering rapidly and strongly in different directions while feeding on flowers) and the audible noise produced by the wings. Since these patterns are atypical for moths, and because tropical organisms are often better known from documentaries than the indigenous Western European fauna, hawk-moths are spontaneously associated to similar patterns characteristic of hummingbirds. The example of humming birds / humming bird hawk-moth is an extreme one and only interesting to illustrate the epistemological aspect of convergent features among non-biologists. For the practical purpose of research carried out to detect convergent evolution in organisms living in a certain environment, the recognition and description of such cases of convergences is widely accepted in biology.

A second reason for the lack of a methodology in the investigation of convergences between distantly related species is that modern biologists tend to specialize in certain groups of organisms (or even in a single species) and to compare the studied species mainly with closely related organisms. This does not apply to all biological disciplines. Ecologists for example, often include a broad range of species in their investigations (Mooney 1977 and other chapters of these two works; see, e.g., Orians & Solbrig 1977b). See also the publications by Raunkiær, Remane, Koepcke, Hesse and several other biologists (discussed above and in Appendix C) in which convergent organisms were investigated in the context of ecological studies.

Some fields have a long tradition of investigations of convergences between distantly related species, as for example the works on organisms adapted to caves (troglomorphs). The conditions of such investigations are ideal, as several extant organisms of different taxa developed convergences to this extreme environment. The heuristic value of these investigations is improved by the possibility of comparing troglomorphs with closely related epigean species, and to compare the degree of troglomorphy between species living in different abiotic conditions. An example of a main factor in hypogean systems is the limited supply of energy when compared with photosynthetically based epigean systems, which is responsible for specific convergent adaptations to food scarcity in troglomorphs (Hüppop 2012).

Finally, modern researchers have the tendency to focus on comparisons between species in which a proper phylogenetic tree is available. This has the positive effect of allowing the use of the phylogenetic comparative method (PCM). The negative effect is that this kind of

investigation ties up considerable research resources and constrains the formulation of research questions and approaches, limiting the possibility of comparisons with more distantly related species. In fact, the comparison between distantly related species can open new perspectives in the research and lead to unexpected insights. Since a convergence approach requires the comparison of traits evolved independently in distantly related taxa, this type of analysis is often difficult to quantify, often impossible to evaluate though statistical methods or to be carried out in connection with very precise phylogeny. In fact, such a precise phylogeny is not only often not possible, but just as often not needed (Ross & Lockwood 2002), as in the analyses of convergent patterns between insects and mammals or mammals and reptiles; this topic will be further discussed in chapter 3).

2.5.3 Different meanings of "clear" adaptive traits

One common use of analogy as a heuristic device for functional interpretation can be found in the investigation of fossil evidence (Abel 1912; 1914; 1924; 1925; Hickman 1988; Rudwick 1964; Seilacher 1974). The use of analogy in palaeobiology implies knowledge of how organismic features are interconnected and functionally organized (Weber 1958). Influential thoughts on this issue were already expressed in pre-Darwinian times, especially by the French naturalist Georges Cuvier (1769-1832) (Coleman 1964; Limoges 1970; Mayr 1982, 182-184, 367-371; Rudwick 1997). I will detour to Cuvier's thoughts on this topic to introduce an example of a wrong assumption on functionality which was expressed by Cuvier's contemporaries and which is still defended in today's biological textbooks (see below, chapter 3.3.2).

Cuvier's work as zoologist and anatomist was based on a comparison of organisms, having in mind their kinship and relationship between organismic structures and their environment. He studied living beings primarily from a functional perspective, searching for original rules with great generality of application. Cuvier was convinced that the study of comparative anatomy is a process analogous to experiments. This conviction was not only implicit in his work, but was explicitly stated, as in following passage from his *Le règne animal*, first published in 1817, here quoted from an English translation by H. McMurtrie:

> The most effectual method of obtaining these [laws of observation], is that of comparison. This consists in successively observing the same bodies in the different positions in which nature places them, or in a mutual comparison of different bodies; until we have ascertained invariable relations between their structures and the phenomena they exhibit. These various bodies are kinds of experiments ready prepared by Nature, who adds to or deducts from each

> of them different parts, just as we might wish to do in our laboratories ; showing us, herself, at the same time their various results. (Cuvier 1831b, vol. 1, 4)

In the first chapter of the *Leçons d'anatomie comparée* (vols. 1-5, first publ. 1800-1805), Cuvier (referring to Kant) explained that the parts of an organism are mutual dependent and intrinsically related to the environment (Cuvier 1835, 5). This "*conditions d'existence*", as he called it in his *Le règne animal*, stated that "nothing can exist without the re-union of those conditions which render its existence possible" (Cuvier 1831b, vol. 1, 3); without using an evolutionary framework, Cuvier's statement sounds today tautological. However, his attempt to analyze traits as part of a whole was a rather unique approach in this time. Also unique was his principle of "*subordination des caractères*", which states that certain features are subordinated to others, allowing us to classify organisms into groups taking into consideration this interrelation (Cuvier 1835, 59-60, 67). As a consequent of these both principles, Cuvier proposed what certainly is the most famous of his generalizations – the principle of correlation of parts (Cuvier 1835, 57).[17] In its more ambitious application it assumes that it is possible on the basis of the fossil of a single bone or even of a fragment of a bone to reconstruct the entire organism. He wrote in his *Discours sur les Révolutions de la Surface du Globe* (here quoted from an English translation):

> Fortunately, comparative anatomy possesses a principle, which, properly developed, was capable of clearing up all embarrassment: it was that of the natural relation of forms in organized beings, by means of which each sort of creature may by rigorous scrutiny, be known by each fragment of each of its parts. Every organized being forms a whole, a unique, and perfect system, the parts of which mutually correspond, and concur in the same definitive action by a reciprocal reaction. None of these parts can change without the whole changing; and consequently each of them, separately considered, points out and marks all the others. (Cuvier 1831a, 58-59)

According to Cuvier's principle of correlations, a carnivore, for example, must have features that work together for the specific purpose of hunting. Consequently, a felid has teeth adapted to slicing flesh along with sharp claws for gripping, holding and debilitating its prey. Through his deep anatomical knowledge Cuvier was often precise in his interpretations of fossil organisms, especially concerning species with adaptive patterns easily recognized as convergent to those of living organisms, even if their functional anatomy diverged from other species of the same taxa. For instance, some early naturalists interpreted the extinct reptile

[17] Cuvier was following a method already suggested by Aristotle. He stated, for example, that animals cannot have at the same time horns and tusks (Hist. anim. II 1, 501 a 15-25).

Pterodactylus as an aquatic animal. In 1830 the German zoologist Johan Georg Wagler published a picture of a reconstructed *Pterodactylus* as an animal analogous to leatherback turtles, eared seals and penguins (Wagler 1830, 72-73). Based only on a drawing by Cosimo A. Collini from 1784 (he never saw the fossil itself), Cuvier was able to recognize it correctly as a flying reptile (Cuvier 1801), an interpretation which was afterwards generally accepted (Taquet & Padian 2004; Wellnhofer 1993).

Cuvier's interpretation of *Pterodactylus* is important to illustrate how convergence is used without a formal methodology in the analysis of organismic features. It is only one of countless examples of the use of non-homologous patterns of similarity related to extreme environmental conditions or highly specialized locomotory or feeding systems for the understanding of the range of organismic adaptation.

However, numerous cases in the organismic world are highly complex, demanding careful analysis of several interpretive aspects of potential convergences. One major difficulty is that non-homologous patterns of similarity do not necessarily imply that the emergence of these traits was due to similar selective pressures. For instance, Darwin had already noted that a large number of flightless birds and insects are found on islands and hypothesized that "powers of flight would be injurious to insects inhabiting a confined locality & expose them to be blown to the sea."[18] Although Darwin was basically right, flightless insects can also evolve in association with several other factors. For example, flightless insects can evolve in the absence of ground-feeding animals or when flying is not required for dispersal or reproductive behaviour. Another factor is related to the costs associated with maintaining wings and flight muscles, or to costs associated with the restricted space a female has available for the storage of her eggs (Carlquist 1966; Hoffmann & Parsons 1997, 101-102; Rankin & Burchsted 1992). It should also be considered that insects living today in certain environments might have lost their flight ability in other environments, e.g., caves (Moldovan 2012; Parzefall 2012).

In several cases, the identification of possible convergences is not the conclusive finding, but the starting point for further investigations. For instance, the function of oversized canines developed independently in non-monophyletic saber-toothed cats is still controversially discussed (see above, chapter 2.4); the reason for this debate is, among others, the lack of similar features in living predators. Even in living organisms, there are several cases in which

[18] Darwin's letter to J. D. Hooker, March 7th, 1855. Retrieved March 31, 2013 from http://www.darwinproject.ac.uk/letter/entry-1643.

non-homologous patterns of similarity are not understood. For example, the adaptive value of the metallic fur colour developed convergently in several subterranean mammals is to our knowledge still unclear (Starck 1961). The same concerns a myriad of non-homologous patterns of similarity, seen for instance in extreme body shapes in insects whose functional meaning is often unknown (Eidmann & Kühlhorn 1970; Resh & Cardé 2003). These examples display a typical aspect of the investigation of adaptations; a closer examination of single hypotheses often unveils new and complex factors, which instigate the formulation of further hypotheses.

Several investigators limit their work on convergences to the identification of possible analogous adaptive traits. Although this intuitive work can be very insightful, subsequent investigations on the emergence and adaptive value of these traits should be done in a more systematic way. Such a methodology aims at clarifying and unifying basic aspects of the investigation, as it concerns objective criteria on the choice of species and traits to be studied. Furthermore, such a method should include an analysis of the evolution of the studied traits in different lineages, focusing on possible constraints in the emergence of these traits or on the identification of possible zigzags in the studied evolutionary lineages.

One of the most important aspects justifying the need for proper methodology in the study of convergences relates to researchers' unconscious tendencies to select information that supports their own hypotheses and beliefs. This phenomenon – called "confirmation bias" (Fanelli 2010; Maccoun 1998; Marsh & Hanlon 2007; Nickerson 1998) – is one of the most definitive factors negatively influencing research. As will be shown in several parts of the present thesis in connection with scenarios proposed to contextualize human evolution, the use of convergence as a tool in evolutionary biology is particularly susceptible to this bias. With the lack of a rigorous and unified methodology, there is ample room for speculations supporting owned views on the form-function relationship of a studied trait.

CHAPTER THREE: CONVERGENCE APPROACH

3.1 Introduction

The here proposed "convergence approach" is defined as *a method in which non-homologous patterns of similarity between two or more distantly related species are used to infer on the functional focus of the traits under investigation*; for a definition and discussion on "functional focus" see below, chapter 3.2. In the literature it is often assumed that traits which are part of clear cases of convergences are probably adaptive. This view is implicit in the work of several biologists and not rarely explicitly formulated, for instance by G. G. Simpson (1972, 132), Wolfgang Wickler (1972, 12) and Hans-Wilhelm Koepcke (1956; 1971; 1973; 1975). In the references quoted in chapter 2.5.1, the use of convergences to gain knowledge is implied or explicitly stated by most authors. In fact, as it is controversially debated which are the internal and external factors responsible for the emergence of parallelisms, it is similarly generally accepted that clear convergent patterns (as between dolphins and sharks, or between cacti and *Euphorbia*) demonstrate how natural selection modifies independently different traits in different organisms to improve their efficiency in the interaction with a certain spectrum of the environment.

The general meaning expressed by Simpson (1972, 132) is followed here – attempts to interpret strong patterns of similarity between distantly related species without assuming the role of natural selection are difficult to defend. This is especially true in cases in which the functionality of traits is clearly associated with the environment. What other than natural selection can explain the fact that distantly related subterranean mammals "are highly specialized and adaptively convergent, both structurally and functionally, for burrowing and living underground in relatively permanent, sealed burrow systems" (Nevo 1999, 78)? Or that "all troglomorphic development [troglomorphs are organisms adapted to life in caves] involves extensive parallelism and convergent evolution" (Christiansen 2012, 527)? The certainty about the adaptive value of specific traits found in subterranean mammals and troglomorphs is linked to the highly unusual traits found in a demanding environment and the absence of such traits in close relative species living outside of this environment (Christiansen 2012; Culver et al. 1995; Howarth 1993; Hüppop 2012; Ma & Zhao 2012; Moldovan 2012). Most conspicuous traits in cave insects are well recognizable as adaptations to life in caves. Examples of troglomorphy are reduction of eyes, pigment, and wings, cuticle thinning (in terrestrial arthropods), hypertrophy of other sense organs, especially tactile organs, and several other physiological traits (Christiansen 2012; Culver et al. 1995, 4-31; Fong 2012;

Howarth 1993; Hüppop 2012; Moldovan 2012; Parzefall 2012; Poulson 2012). Cave insects also display certain typical traits which are not well understood; for example, some troglomorphic species (pholeuonoids) have a spindle-shaped abdomen and a neck-shaped prothorax (Moldovan 2012; Sket 2012; Weber 1954). Although the functionality of such traits is not unravelled, it is sensible to assume as a working hypothesis that these traits are the product of natural selection and therefore also adaptations to cave environment. There are also cases in which it is difficult to establish if troglomorphic features are derived or ancestral character states (Fong 2012).

What is valid for troglomorphic organisms also applies to conspicuous cases of convergences in organisms adapted to other extreme environments, such as sea ice, polar terrestrial environments, high altitude and latitude lakes, polar and hot deserts, terrestrial hydrothermal environments, deep sea, hypersaline, hypoxic and anthropogenic extreme environments (Bell & Callaghan 2012 and other chapters from the same volume; Hoffmann & Parsons 1997; Wharton 2002). In sum, it is assumed here that "clear" cases of convergences is a valid term when it refers to non-homologous patterns of similarity where non-adaptive functional relationships would appear as highly artificial. The classification between „clear" and „less clear" cases of convergences is not only dependent on the characteristics of the organisms, but also from our knowledge of the functional meaning of traits and our modified perception after the acquisition of this new knowledge. Darwin already pointed out the difficulty of recognizing the aquatic behaviour of dippers (*Cinclus*) from their anatomy: "[T]he acutest observer by examining the dead body of the water-ouzel would never have suspected its sub-aquatic habits; yet this anomalous member of the strictly terrestrial thrush family wholly subsists by diving,—grasping the stones with its feet and using its wings under water" (Darwin 1859, 185). Although dippers do not have clearly recognizable features typically found in other aquatic birds – like penguins or auks (Alcidae) – several anatomical traits in these birds are considered today as adaptive for swimming and hunting underwater, like underwater vision (Goodge 1960) and short/strong wings (Haffer 1985).This is an important aspect of functional analyses: the researcher's ability to recognize patterns of functionality increases after more careful analyses of traits. This increased ability to recognize patterns is a general characteristic of human cognition. As stated by Chalmers, "what observers see, the subjective experiences that they undergo, when viewing an object or scene is not determined solely by the images on their retinas but depends also on the experience, knowledge, expectations and general inner state of the observer" (Chalmers 1992, 26); see also example by Polanyi (1974, 111).

However, there are several problems related to the fact that the analysis of non-homologous patterns of similarity between distantly related species is not formalized. For example, it is often not clear how the functional inferences in fossil or extant vertebrates can be used to corroborate the evolutionary scenarios. A further problem is related to assumptions and oversimplifications in functional interpretations which are not explicitly stated.

These and other problems are especially recognizable in scenarios proposed to contextualize early hominin evolution (see Appendix D and chapter 6).

3.2 Functional focus

The term "functional focus" for discussions on adaptive traits is suggested here and defined as follows: *The total pattern of adaptive and non-adaptive features of an organism which is effectively used or can be used under certain circumstances in its interaction with the environment.* The term "focus" here draws an analogy to the same term used in optics: we are able to focus an image partially, having out of focus other parts of the image. Analogous to this, an organism "focuses" with its morphological, behavioural and physiological traits on some aspects of the environment strongly and is "out of focus" to different degrees with other aspects of the environment. The functional focus emphasises that an organism will usually be able to develop a better performance in connection with a specific interaction with the environment by losing efficiency in the interaction with other aspects of the environment – a phenomenon commonly named trade-off. The classical usage of the term "effect" is followed here, as used by other authors (Simpson 1946, 84; Williams 1966, 6-8), who referred to traits which were probably not selected for a current function. This term was expanded for traits in which we cannot be sure if they were built to perform the current function.

3.2.1 Examples: hippopotamuses, elephants, penguins, and turtles

Adult hippopotamuses (*Hippopotamus amphibius*) are usually considered as not able to swim in fresh water. Due to their negative buoyancy they "walk" or "gallop" along river and lake bottoms (Coughlin & Fish 2009; Fisher et al. 2007; Klingel 1988). However, there are indications that they are able to swim in sea water, as suggested by their geographical distribution (Frädrich 1967; Frädrich 1968; Hadjisterkotis et al. 2000; Klingel 1988; Schüle 1993; Sondaar 1986; van der Geer et al. 2010, 24). On South African coasts, isolated

hippopotamus are occasionally observed in the sea.[19] We do not have evidence that this ability to swim in salt water was ever specifically selected, so we call this ability an effect. Another example concerns elephants. They are known as excellent swimmers (Johnson 1980a; Tobias 2002a). They have been observed using their trunks as snorkels while swimming (Altevogt 1987; Schüle 1993). We do not know how Proboscidea used their trunks in the past, and we do not know if the use of trunks as snorkels by extant elephants was specifically selected for this purpose. However, although we will probably never know the most relevant steps in the emergence of this trait, it seems fairly sensible to assume that this specific use of the trunk in extant elephants is important – it is part of their functional focus. Natural selection can perhaps be assumed for this specific function, but not conclusively.

An interesting example concerns non-aquatic locomotory patterns in extant penguins. Penguins are highly specialized wing-propelled divers and swimmers. In their evolution the flight apparatus was modified to meet the demands of locomotion in water. The adaptive traits linked to swimming and diving are recognizable among others in the fusiform body shape, in the compact flipper-like wings with strongly reduced articular mobility, in the lack of differentiation in the wing feathers, the layer of blubber and the extremely numerous feathers on the body (1986a; Bannasch 1986b; Kristoffersen 2001; Simpson 1946; Storer 1971). In several diving birds, morphological changes in hindlimbs reflect swimming and diving adaptation (Feduccia 1987; Heilmann 1926; Storer 1971). Storer explained the convergent morphological changes found in foot-propelled divers, loons, grebes and the extinct Hesperornithiformes as follows:

> The femora and the tibiotarsi lie nearly in the frontal plane passing through the acetabula, and all but the distal ends of the tibiotarsi lie within the main body mass. Both stabilizing breadth and "streamlining" are provided by this arrangement, which also results in placing the feet near the posterior end of the body. (Storer 1960, 701)

Also in penguins the feet are placed near the posterior end of the body, as they are used in steering during swimming. Penguins have a conspicuous upright posture and it is well known that they also locomote in this position. An almost upright stance evolved convergently in several other aquatic birds. Examples are the extinct flightless Great auk (*Pinguinus impennis*), the common murrre (*Uria aalge*) and other auks (Alcidae), and cormorants, like the flightless Galapagos cormorant (*Phalacrocorax harrisi*). As in penguins, it is commonly

[19] See http://www.dailymail.co.uk/news/article-1022276/Pictured-The-hippo-ditched-muddy-waters-catch-sun-surf.html.

assumed that this upright posture is the result of the legs being positioned near the posterior end of the body; see Bender (1999, 130-131) for illustrations showing postural differences between terrestrial and aquatic birds.

Simpson in his general theory of penguin evolution, referred to this topic. He remarked that the several aquatic features interact in a complicated way and it is impossible to isolate them. He wrote:

> They can only be considered as factors simultaneously involved in the integrated organism. Nevertheless, it seems probable that the adaptations for terrestrial locomotion in an upright posture, that is to say, the ways in which these differ from the normal walking adaptations of flying birds, are secondary and are in one sense are result of the swimming adaptation. The foot and leg structure of the penguins is a primary adaptation to their method of locomotion and of standing, but the differences between this method and that of other birds probably arose in connection with the completion of their aquatic adaptation. (Simpson 1946, 84)

To be able to walk, penguins have to stand upright a keep to the centre of gravity above the feet. Penguins also show specific modifications in their locomotion on land, as Simpson explains:

> In this connection, the penguin's alternative mode of land locomotion, sometimes called "tobogganing", is of interest. The penguins slide alone on their breasts and bellies, propelled by strokes of the wings and feet, achieving on a suited surface, a greater maximum speed than when running upright. This mode of progression is very nearly swimming on land, except that it does still depend heavily on the feet, which are almost wholly passive in submarine swimming. (Simpson 1946, 84)

Some penguins, like the southern rockhopper penguins (*Eduyptes chrysocome*), jump with both feet along steep, rocky slopes and use a similar gait when moving faster on flat land. It is perhaps reasonable to assume that this gait is adaptive to climb steep slopes, but how adaptive is the same gait when used on flat land? Or how adaptive is the tobogganing? Even if we consider tobogganing and hopping as mere effects of the aquatic adaptations in penguins, these traits illustrate how new features can emerge: phylogenetic constraints – or morphological bias (Ross & Lockwood 2002, 17) – can lead to new behavioural patterns used irregularly by single individuals of a population. If these behavioural traits represent an advantage compared to the usual behaviour (such as by minimizing costs related to terrestrial locomotion) they can in subsequent steps be optimized through natural selection. The concept

of natural selection as primarily a process of optimization is often implied by modern biologists. This concept was explicitly stated by Alexander:

> A shopper looking for the best buy chooses the cheapest article among several of equal quality, or the best among several of equal prices. Similarly, natural selection favours sets of genes which minimize costs or maximize benefits. The costs can often be identified as mortality or energy losses, the benefits as fecundity or energy gains. Optimization is the process of minimizing costs or maximizing benefits, or obtaining the best possible compromise between two. Evolution by natural selection is a process of optimization. (Alexander 1996, 2)

The upright posture is not the only solution for terrestrial locomotion in secondary aquatic vertebrates having the feet placed near the posterior end of the body where they are used in steering and propulsion in water. Some of these animals are only able to crawl on their bellies on land. This applies, for example, to the red-throated loon (*Gavia stellata*) (Burton & Demuth 1985, 27); also the ruddy duck (*Oxyura jamaicensis*) is described as clumsy during locomotion on land (Raikow 1970, 5). Raikow compared the birds of the genus *Podiceps* (highly specialized in swimming and diving) with pinnipeds (semiaquatic marine mammals) concerning their helpless locomotion on land; see also Bender (1999, 149-152).

A higher degree of certainty in functional analyses can be expected in traits which evolve under strong selective pressure to perform a certain function, such as flippers, which are the propelling agents in penguins. If interspecific variation in the length or form of flippers deviate considerably from the values found in closely related species, and if this variation can be correlated with certain environmental conditions, there is a strong indication that this association is adaptive. In his investigation of the general biology and thermal balances of penguins, Stonehouse (1967) observed that four species of penguins[20] have 10 % greater flippers than the theoretical value for their weight. He saw this deviation as a thermoregulatory adaptation to warmer environments (shedding heat).

These and other examples demonstrate that penguins' morphological adaptations reflect a trade-off between swimming efficiency and mobility on land (Pinshow et al. 1977) and several other aspects related to their biology (Boersma 1975; Müller-Schwarze & Müller-Schwarze 1975; Stonehouse 1967; Stonehouse 1975). Penguins'adaptive traits illustrate a crucial aspect of the convergence approach: the use of analogy to gain knowledge in adaptive

[20] Humboldt penguin (*Spheniscus humboldti*), African penguin (*Spheniscus demersus*), erect-crested penguin (*Eudyptes sclateri*), the fairy penguin (*Eudyptula minor novaehollandiae*), and the Chatham Island subspecies of the blue penguin (*Eudyptula minor chathamensis*).

analysis should be based on objective criteria concerning the choice of species used in comparisons. In the case of mobility on land in penguins, the terrestrial locomotion should not be compared with fully terrestrial species, but with other semi-aquatic vertebrates which show similar trade-offs; see also following example of digging capability and terrestrial locomotion in green turtles.

In his influential paper *Adaptation*, Richard C. Lewontin used several examples in his criticism of the so-called "adaptationist program". One of the hypotheses of this paper was that "Every trait is involved in a variety of functions, and yet one would not want to say that the character is an adaptation for all of them" (Lewontin 1978, 164). To illustrate this point he mentioned the behaviour of the large marine turtles known as green sea turtles (*Chelonia mydas)*. The females of this species drag themselves up the beach with their front flippers and spend many hours digging a deep hole for their eggs with their hind flippers. Lewontin concluded, "No one who has watched this painful process would describe the turtles' flippers as adaptations for land locomotion and digging; the animals move on land and dig with their flippers because nothing better is available" (Lewontin 1978, 164).

Lewontin's statements imply a comparison between green turtles and other organisms more proficient at digging holes (like some terrestrial mammals). This implication ignores the fact that the females' ability to dig holes – not to dig fast or elegantly, but to dig holes - was under strong selective pressure, since green turtles that are not able to dig cannot reproduce. Here we find a completely different situation than the penguins' tobogganing: although several aspects of the evolution of turtles remain obscure, we have good reasons to assume that although the selective pressure on the green turtles' hind limbs was primarily acting on the function of steering, the optimality of this trait for this function was imperatively constrained by the function of digging. This trade-off is also mentioned by researchers who studied the size differences in hind limbs in two different populations of this species. Concluding their investigation, the authors state that beside the steering function of the hind limb, the morphology of this organ "is constrained by both their evolutionary history (modification of the basic turtle foot plan) and other essential limb functions, such as crawling, nest construction (for females), or grasping during mating (for males)" (Wyneken *et al.* 1999, 495). The performance of green turtle's hind limbs to move on land and to dig holes cannot be evaluated through a comparison with distantly related species able to move well on land and to efficiently dig holes in the sand, but with closely or distantly related species showing comparable anatomical and physiological constraints. The concept of functional focus

acknowledges the complexity of the evolutionary steps of traits with all the uncertainties related to specific selective pressures acting on different traits and trade-offs resulting from the interplay between traits. It recognizes that our ability to investigate these complexities is limited, but at the same time establishes (as the concept is imbedded in the convergence approach) that natural selection is a main factor in the shaping of traits which have convergent counterparts in other organisms.

3.2.2 Natural selection in behavioural traits: examples of domestic animals

In Morocco, domestic goats (*Capra aegagrus hircus*) often climb on Argan trees (*Argania spinosa*) in search of food. Photos[21] with a tree occupied by ten or more goats are often regarded as fakes by non-specialists with a healthy scepticism. However, video material[22] shows that this behaviour is real. For these goats, the ability to climb on trees is probably an important aspect of their functional focus, as food in this region is scarce. However, it is reasonable to assume that the ability to climb trees was primarily shaped in connection with the mountain habitats of wild goats (*Capra aegagrus*) ancestor – climbing on rocks and not on trees.

Another example of the difficulty of evaluating the role of natural selection for the emergence of a behavioural trait in domestic mammals is the pronounced variation within the domestic cat (*Felis catus*) in its readiness to take to water. Most pet owners would probably agree that their cats avoid bodily contact with water – apart from drinking. There are however exceptions to this pattern: single observations of fishing in domestic cats were reported (Gudger 1925; Leyhausen 1996, 91), and the Turkish natural breed Van (named after the Lake Van in east Turkey) is said to enter the water readily and even to hunt fish in lakes or rivers (Loxton 1976, 136-137). As usually stated in popular literature, this breed is thought to show this behaviour as an adaptation to the harsh environment in east Turkey, where fishing might be necessary to obtain enough food. In a study comparing five Van cats to five ordinary domestic cats, Widmer showed that Van cats interacted more intensively with water (Widmer 1990). In 2002 Bender and Hirt tested experimentally the readiness to enter water in a group of Van cats (n=17) and compared it to a group of another domestic cat breed, the Russian Blue cat (n=9). Both cat groups were kept in similar conditions and never experienced water bodies other than their drinking bowls. The cats were lured to enter a 1x1 meter swimming pool with 6 cm water, in order to reach food or a toy. The Van cats showed significantly more

[21] See http://webecoist.momtastic.com/2008/08/19/the-incredible-tree-climbing-goats-of-morocco/, retrieved on 3th March 2014.
[22] See https://www.youtube.com/watch?v=oQev3UoGp2M, retrieved on 3th March 2014.

often water contact than the Russian Blue cats (16 Van cats vs. 2 Russian Blue cats, $p<0.001$), with two Van cats wading completely through the water until reaching the food. No Russian Blue cat put its paw completely into the water (Bender & Hirt 2002). It is possible that the readiness to enter water or to play with water in the Van cat is a product of selective pressures related to fishing (as stated above, the Van cat is a natural breed). However, this behaviour can also be interpreted as an effect of what seems to be a very playful and active character of this breed (also in the adults) when compared with most other breeds (personal observation). An alternative hypothesis is that several components were involved in this behaviour – selective pressure related to fishing, a playful and active personality shaped by natural selection or by selective breeding, or both (Nicole Bender, personal communication). These examples serve to illustrate the differences between the terms "adaptation" and "functional focus", which can be seen in following fictitious sentence: "In certain regions of Morocco, goats are adapted to eat on trees". By recognizing the difficulties in establishing the real selective factors shaping this behaviour, I prefer the sentence: "In certain regions of Morocco, eating on trees is part of the functional focus of goats". This term acknowledges the fact that these populations are ascending regularly trees, without assuming certainty about specific selective pressures in the differences in climbing trees between these and other goats. Although the main hypothesis is that "climbing" (trees, fences, rocks, whatever) was shaped by natural selection in connection with mountain habitats (where trees probably did not play any role), it cannot be completely excluded that in the Moroccan goats the ability to climb on trees is optimized when compared with the same ability in other goats. This is a simple example. When discussing the emergence of traits in most organisms, the situation is often much more complex, for example by uncertainties on the direction of evolutionary steps.

3.2.3 Uncertainties concerning selective pressures shaping swimming ability in humans

Humans are not able to swim instinctively, but they are able to learn to swim and regularly do so under certain environmental conditions (see chapter 5). However, this isolated fact cannot be used as conclusive evidence that humans were under selective pressure in the past to swim. As it will be shown elsewhere (chapter 4.2.6), although swimming ability is a widespread trait in mammals (also in primates), non-human hominoids are usually not able to swim, which indicates that a common ancestor of all living hominoids lost the ability to swim instinctively. To date, confirmed data on swimming and diving exists only for one common chimpanzee (*Pan troglodytes*) and one orangutan (*Pongo pygmaeus*) living in captivity (Bender & Bender 2013); this emphasises the possibility that in hominoids the ability to swim is not dependent on selective pressure for this specific behavioural trait. However, even considering that we

ignore evolutionary events leading to the tendency of modern humans to interact more frequently with large bodies of water, it is conceivable to assume that the ability to swim (e.g. for crossing rivers, foraging in water, etc.) is important for individuals of certain populations in which swimming and diving are regular behaviours. The term “important” refers to the obvious role of swimming for preventing drowning when crossing rivers or exploring aquatic resources. With the term “functional focus” our ignorance about the evolutionary factors responsible for the widespread behaviour of swimming in humans is expressed, as well as our ignorance about the exact degree of advantage that swimming behaviour actually represents to humans able to swim, when compared with individuals not able to swim. The term functional focus does not imply that the ability to learn to swim in humans was shaped or not by natural selection for this specific behaviour, but acknowledges the fact that in humans and some (perhaps all) non-human hominoids there is no anatomical or behavioural barrier to the development of this ability. As we will see later, it is possible that the divergence between humans and non-human hominoids relative to how often they learn to swim is associated to other, “dry” aspects of human biological and cultural adaptation.

3.2.4 Underwater vision in humans

In some cases it is not clear if a particular difference in a trait between two species or between two populations of the same species in a trait was selected to perform a function (= an evolutionary adaptation) or is the result of short-term physiological responses. An interesting example is the underwater vision in terrestrial animals. Several animals see well both underwater and above water, as they have spherically corrected lenses (Dral 1985; Land 1987) – this ability is definitively an adaptive trait to improve visual accuracy underwater without losing the ability to see well in air. Concerning vision, modern humans do not belong to this category of amphibious animals. Most people know from experience that underwater vision in humans is severely defocused. It seems that today’s humans do not show a better accuracy for underwater vision than, for instance, orangutans. As will be shown in chapter 4.2.4, I observed an orangutan picking up small objects (candies) from the bottom of a swimming pool without visual aids; the same degree of visual (in-) accuracy underwater should be expected from other non-human hominoids. The ultimate cause for this loss of visual accuracy underwater, when compared with above the surface vision, is because humans (as most primates) have a long evolutionary history of using their eyes primarily for orientation in terrestrial environments. The proximate explanation refers to the anatomy of the human eye. The corneal surface accounts for two-thirds of the eye's refractive power. Underwater vision is poor in humans, as the cornea and the aqueous humour of the human eye

have about the same refractive index as water. As result, the eye loses about two-thirds of its refractive power when we enter water, and the image underwater becomes severely unfocused – small objects remain unresolved for most humans (Gislén & Gislén 2004; Martin 1985).

Although our vision does not point to a semi-aquatic phase in our phylogeny, is it perhaps possible that some human populations have a more accurate underwater vision due to natural selection? Researchers noted that children from some tribes of sea gypsies (populations living in Southeast Asia and living off the sea) are very skilled at collecting food from the sea floor without the use of visual aids. Gislén and co-workers have measured the visual acuity of six children in the Moken sea gypsy population and compared their visual acuity with that of 28 European children in the same age range. They found that in the Moken children the underwater acuity is more than twice as good as that of European children (Gislén *et al.* 2003). However, this difference in their underwater vision is probably not the result of selective pressure for better underwater vision in the Moken. The same research group found that through experiments European children can achieve the same underwater acuity as the Moken children after one month of underwater training. According to the researchers, the improved underwater acuity can be explained by the combined effect of pupil constriction and a strong accommodation (Gislén *et al.* 2006).

3.3 Functional changes, premises and assumptions in adaptive analysis

3.3.1 Premises implied in hypotheses on adaptive traits

How can the concept of functional focus contribute to the above mentioned dichotomy between non-historical and historical approaches to the topic adaptation? Adaptive focus implies that historical aspects are always relevant and they have always to be investigated when possible. It implies also that it is important to declare the limitations of our methods in the discussion of adaptations. I would like to return to the above mentioned paper by Gould and Vrba to explain this point and link it to the concept of functional focus.

When discussing the current need for a concept of exaptation, they assumed that “the distinction between ad- and exaptation, however difficult, is not unresolvable. If we ever find a small running dinosaur, ancestral to birds and clothed with feathers, we will know that early feathers were exaptations, not adaptations, for flight” (Gould & Vrba 1982, 7). This statement is important as it stresses the difficulties of proposing new terminology to make a discussion more precise (this alleged increasing precision is here questioned). On the other hand, it demonstrates the problems of meeting the high standards required to fulfil the rigour of this

terminology. To underline this point, I suggest re-formulating Gould and Vrba's statement quoted above:

"If we ever find a small running dinosaur, ancestral to birds and clothed with feathers, we will know that early feathers were exaptations, not adaptations, for flight" (Gould and Vrba, quoted above), if:

(a) ... we would be able to exclude the possibility that this dinosaur descended from a flying feathered dinosaur and therefore secondary adapted to a terrestrial form of locomotion (the loss of flying ability occurred several times in the phylogeny of modern birds) and if

(b) ... we would be able to exclude the possibility that this dinosaur is a convergent form to the ancestor of birds. In the case that a convergent form cannot be excluded, it would weaken the use of this organism to infer on the emergence of flying in birds.

This is, however, only one problem with the differentiation of adaptation/exaptation. In the next section Gould and Vrba illustrated the use of the term exaptation through a hypothesis on the use of feathers in other context than flying. They quoted Ostrom, who wrote on the possibility that an enlargement of feathers in the narrow hands of an ancestor of *Archaeopteryx* might have been to increase the hand surface area, thereby making it more effective in catching insects; in a secondary phase, so Ostrom, changes in specific anatomical and neuromotor patterns resulted in the evolution of flight (Ostrom 1975). Gould and Vrba noted that they do not assert the correctness of these hypotheses, aiming only at an examination of appropriate terminology for a common set of hypotheses – I am referring to this example for the same purpose; we will return to Ostrom's ideas shortly.

Furthermore, Gould and Vrba wrote on the black heron (*Egretta ardesiaca*) of Africa, which, like most modern birds, uses its wings in flight, but also uses them to prey on small fish through an unconventional strategy. They quoted following sentence from a classical book on South African birds: "Its fishing is performed standing in shallow water with wings stretched out and forward, forming an umbrella-like canopy which casts a shadow on the water. In this way its food can be seen" (McLachlan & Liversidge 1978, 39). Gould and Vrba[23] linked the discussed examples with their new terminology:

> We see, in this scenario, a sequential set of adaptations, each converted to an exaptation of different effect that sets the basis for a subsequent adaptation. By this interplay, a major

[23] See also Thulborn and Hamley (1985), who proposed a similar hypothesis.

> evolutionary transformation occurs that probably could not have arisen by purely increasing adaptation. Thus, the basic design of feathers is an adaptation for thermoregulation and, later, an exaptation for catching insects. The development of large contour feathers and their arrangement on the arm arise as adaptations for insect catching and become exaptations for flight. Mantling behavior uses wings that arose as an adaptation for flight. The neuromotor modifications governing mantling behavior, and therefore the mantling posture, are adaptations for fishing. The wing per se is an adaptation in its current effect of shading, just as the feathers covering it also arose in different adaptive contexts but have provided much evolutionary flexibility for other uses during the evolution of birds. (Gould & Vrba 1982, 8)

A closer look of the examples used to illustrate the term exaptation shows interesting theoretical difficulties. A main problem is that a clear differentiation between exaptation and adaptation is always dependent on the assumption of the functional role of a certain feature. In the example above, for instance, Gould and Vrba assume that the initial conditions of the traits “feathers”, “elongated feathers” and “mantling behaviour” are known. However, the initial conditions of every preliminary stage in the sequential set of adaptations exposed by Gould and Vrba are obscure, and specific statements on the functional role implied in these examples are imprecise for several reasons:

(a) Thermoregulation is one of the possible explanations for the emergence of feathers, but by far not the only one. It is possible that other factors were relevant for the initial steps previous to the stages in which feathers were developed to fulfil the minimal conditions necessary to regard this trait as having an effect on thermoregulation. For instance, a small modification of an isolated group of proto-feathers in connection with an unknown reason would change the designation of “feathers as adaptation for thermoregulation” in the above depicted scenario; see also the reviews of hypotheses on the evolution of feathers and evolution of flight (Bock 2000; Shipman 1999; Videler 2006, passim).

(b) The use of Ostrom’s hypothesis is problematic for other, also insightful reasons. First, the assumption of an enlarged surface to improve the function of catching insects lacks analogical evidence from other living organisms, for a simple reason: enlarged feathers are not suited for this purpose. This trait would perhaps make sense when suggesting that enlarged feathers might provoke turbulence to disorientate for a short period of time flying insects, facilitating their predation, or to constrain the insects, as observed in bats. Bats can take their prey directly with the mouth, but often they use the wings as voluminous structures to constrain and direct the insects towards the mouth (Gebhard 1997, 163). The use of an enlarged surface would also be theoretically possible (although not very convincing) in the context of a web

like construction (in analogy with a spider web). However, in these hypothetical cases the question of initial structures is not answered, and Gould and Vrba did not touch the questions concerning the poor analogy implied in Ostrom's hypothesis and the question of selective pressures responsible for the evolution of proto-wings "before" they could be used to prey on insects. A few years later, Larry Martin criticized Ostrom's hypothesis, arguing that the idea of feathers as an insect net is weak (Martin 1983, 122). Ostrom later agreed with his critics, suggesting instead that 'Proavis' caught insects with its teeth, using its proto-wings to allow leaps into the air; see references and discussion in Shipman (1999).

(c) The same problem concerning assumptions on functionality of a certain trait can also be found in the example of mantling behaviour. As we saw, Gould and Vrba quoted a passage of MacLachland and Liversidge's book in which they expressed the idea that the shadow created by the wings allow the birds to see the fishes. As Gould and Vrba stated, they did not assert the correctness of this and the other hypotheses – but they saw the example as good enough to be used to illustrate the use of their new terminology – so they were at least not chosen as negative examples of an adaptationist programme. However, the mantling behaviour cannot be regarded only from the perspective of "use of wings to fly" and "use of wings for fishing". There are several possibilities arguing for mantling behaviour as being shaped in connection with other selective pressures for other functions and only in a secondary step been modified for the specific purpose of fishing. For instance, mantling-like behaviours are observed in several birds for the function of protecting eggs and chicks. Beside the famous example of ostriches, I mention only two further examples: in the vulture *Torgos tracheliotus* for the purpose of protection from the sun (Shobrak 2001), or in the yellowhammer (*Emberiza citrinella)* for the same reason (Blotzheim & Bauer 1997, 479-480). Mantling is also known in several raptors to shield their prey from competitors that might be potential thieves, as in the boreal owl (*Aegolius funereus*) (Mebs & Scherzinger 2000, 43) and other raptors. Spread wings is also common in threat display, as in the long-eared owl (*Asio otus*) (Mebs & Scherzinger 2000, 49) and very common in mating display. Spread wings are also often observed as part of posturing behaviour in connection with thermoregulatory purposes; see Jenkins (1988) for postural behaviour of nestling bald eagles (*Haliaeetus leucocephalus*) and Potter and Hauser (1974) for sunbathing and anting in birds (in relation to molting).

Gould and Vrba acknowledge in the sentence quoted above that the wing and the feathers covering it "have provided much evolutionary flexibility for other uses during the evolution of birds" (Gould & Vrba 1982, 8), but they do not refer to how this flexibility affects the

application of their terminology; the rigour of the terminology is not present in these few examples. Additionally, the specific idea expressed by MacLachland and Liversidge on the use of the wings to see the fish can be refined: although the possibility of improving visibility belongs to the main hypotheses expressed in connection to this behaviour, other equally important factors were also mentioned in the literature; for example, the effect of the umbrella to cast a shadow to *attract* the fish in this specific area where they can be preyed upon; see discussion and further references in Irwin (1975).

The thoughts above show the problems of proposing hypotheses based on weak or imprecise assumptions on the functionality of a certain trait. As expressed by Dennett when he commented on the problems related to the term exaptation: " But, according to orthodox Darwinism, every adaptation is one sort of exaptation or the other – this is trivial, since no function is eternal; if you go back far enough, you will find that every adaptation has developed out of predecessor structures each of which either had some other use or no use at all" (Dennett 1996, 281); see also Dennett (1998). Every statement labelling a trait in the dichotomy adaptation/exaptation without a precise formulation of the initial conditions of the considered trait can be easily modified by using a stronger level of magnification and by the inclusion of more realistic alternatives for the proposed functional analysis. This will often lead to an inversion of the classification adaption/exaptation. For this reason, instead of labelling traits as exaptations or adaptations, in most cases I prefer to focus on a careful formulation of premises implied in hypotheses on adaptive traits, making special efforts in the clarification of which are the pre-conditions needed for a certain trait to be selected for a specific function. Furthermore, I consider wherever possible the use of convergence as a tool to evaluate organismic form-function relationship in these analyses. The whole approach is conceived in a way that allows a greater transparency concerning our limits and possibilities to reconstruct evolutionary events. This transparency should avoid, among others, the pitfalls of assuming knowledge on evolutionary events where no empirical evidence justifies such an assumption – a problem which will be discussed in detail in connection with palaeoanthropological hypotheses.

3.3.2 Minimal preconditions of a trait to perform a function

The use of analogies between organisms and simple machines are not unusual in discussions on the interpretation of fossil data (Hickman 2004; 1988; Rudwick 1964; Seilacher 1974; Weber 1958). The study of organisms aiming at a transfer of technology between them and engineering systems (in bionics) is well-known (Hill 2001), and the use of analogies between

biological structures and human technology is ubiquitous in research and demonstration of biological function from a biomechanical point of view (Borelli 1978 (first published 1680); Vogel 1989; 1998a; 1998b; 2001; 2006; 2007; 2009). Similarly, a thought experiment with a simple piece of human technology is proposed here to discuss certain aspects related to the evolution of adaptive and non-adaptive traits and to the formulation of hypotheses on the evolution of such traits.

A human plans a device on which to hang his jacket. He finds a piece of metal which could be used for this purpose, attaches it to the wall and recognizes that the hook in its actual condition is not functional for the purpose of hanging clothes. He uses a hammer to stepwise improve the functionality of this proto-hook until the piece is finally modified to a point at which functionality is reached – a jacket hangs on the piece. Several traits in organisms – let's say the wings of insects – could not initially evolve by natural selection for the function of flight before fulfilling certain minimal preconditions, for example concerning size. This means that small winglets must certainly have had a different function (or no function at all) before they reached the point at which natural selection could begin to improve the performance of these structures "as wings". I suggest the term *'interlocking point' to label the stage in which a trait or a set of traits fulfils the minimal preconditions to perform a given function*. In the case of a piece used to hang clothes, these preconditions are easy to establish. In the case of wings in insects the problems are more complex. Several hypotheses have been proposed to explain which selective advantages winglets would have before reaching the point at which these structures had significant aerodynamic effects; one of the main hypotheses is based on thermoregulation and isometric changes in body size (but not in body form) (Kingslover & Koehl 1985).

One of the major problems when investigating adaptive traits is related to the assumptions about the functionality of the studied traits at different stages of their evolution. As shown in Fig. 3.1, it is possible that we are starting from a wrong assumption on fundamental aspects of the biological role of traits. To use the above example of the hook, the gradual steps needed to change the piece until it reaches the interlocking point become superfluous, if the spatial orientation of the proto-hook on the wall is radically changed – the piece was already a hook, it was just turned upside-down. The same applies to our ability to differentiate between physiological and non-physiological spatial orientation of organisms. Fig. 3.1 (c) and (d) depict two illustrations of sloths taken from two different natural history books from the pre-Darwinian period. Although sloths can also sit on top of branches, they do not stand on them

as in (c) and (d). The mistaken position of both sloths is probably explained by the fact that the typesetters used their knowledge of terrestrial mammals (like squirrels and cats) for their decisions in turning the illustrations and depicting sloths like arboreal quadrupeds. Fig. 3.1 (f) and (g) shows what is probably the original intention of the artists depicting sloths in natural environments – using their highly specialized curved claws not to stand on branches, but to hang.



(a)



(c)



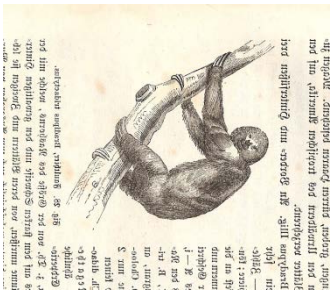
(e)



(b)



(d)



(f)

Figure 3.1 Wrong assumptions on fundamental aspects of the biological role of traits. It is important to correctly interpret the initial state of the considered traits; this applies both to human technology as well as to biological structures. In the case of the hook, the whole procedure with the hammer acting on the structure spatially oriented as in (a) would be unnecessary with the initial state as depicted in (b). How organisms can be wrongly interpreted is illustrated by following pictures of sloths. (c) and (d) are depicted in books on natural history from the mid-19th century. These illustrations were probably conceived to be published oriented as in (e) and (f). I found these two cases in books of my own library. It is predicted here that a systematic search in natural history books of this period would reveal further cases of sloths wrongly depicted. (c) and (e) from Baumann (1837, 519); (d) and (f) from Agassiz (1855, 85).

Wrong interpretations of living organisms also take place in palaeoanthropological textbooks (see examples in Appendix D) or catalogues of museums of natural history, as for instance in connection with flying fishes; we have here to make a detour to the historical roots of this episode, which is related to Cuvier's principle of correlation of parts.

Although Cuvier denied evolutionary changes in organisms, his "*loi de corrélation des forms*" was extremely successful, and the concept is sporadically mentioned by modern biologists with historical awareness as one with strong heuristic value but with limitations (Coleman 1964, 119-120; Mayr 1982, 460; Rudwick 1976, 113). There are multiple reasons for the

success of this concept. Firstly, it stressed the adaptive relationship between organisms and their environment in a time when anatomists were increasingly carrying out a more descriptive anatomy; secondly, it could be applied to all organisms; thirdly, it was compatible with the need of empirical approaches of this time; and finally it expressed new facets of the old idea of a harmonious universe. Cuvier's method reflects the enthusiastic confidence in the use of experiment, logic, accurate observation and adequate instruments to solve intricate problems. The more intricate the problem, the greater was the challenge and the rewards of the enterprise. Cuvier's views had a long-term influence on comparative anatomy and zoology, not only in the discourse of the 19th century, but also in the century to follow. It is not surprising that Cuvier's concept failed in the reconstruction of "unusual" or "bizarre" fossil organisms. These adjectives refer to organisms with a combination of features which are not known in extant species, as for example, the extinct clawed perissodactyls commonly referred as chalicotheres, with heads similar to those of horses but with large claws on the feet (see Prothero & Schoch 2002, 247-253). This example illustrates a crucial aspect in the use of convergence as a tool – the importance of analysis of analogous adaptive features among living organisms to understand fragmentary evidence of extinct species.

The principle of correlation of parts is mentioned today in different contexts, been stressed positively or negatively according to different perspectives motivated by different research programs. Researchers working with modularity in development and evolution, for example, might mention Cuvier's view of organisms as antithesis, as for instance by Schlosser and Wagner (2004, 1). On the other hand, although Cuvier's principle of correlation certainly does not hold in its exaggerated form, the idea that parts of an organism act as integrated wholes that work together is crucial in biology. Cuvier is rarely quoted by modern biologists in connection with such concepts, but his strong influence[24] is perceptible in the theoretical and practical palaeobiological research – for instance concerning the use of analogy in the interpretation of fossil record (Hickman 1988; Lugar 1990; Rudwick 1964; Seilacher 1974), in discussions on the coordination of characters from an adaptive point of view (Grant 1963, 114-117), or in evolutionary concepts which stress the importance of interpreting single traits not as isolated but as part of the whole organism; this applies for example to Le Gros Clark's

[24] A similar view was also expressed by David B. Weishampel, who wrote: "In paleontological functional morphology, studies that use analogy have a long and rich history, dating at least to Cuvier's conceptualization of correlation of parts, and they certainly have remained strong to the present day" (Weishampel 1997, 35).

concept of the "total morphological pattern" [25] (Clark 1964), redefined by Tobias (1985) and used by Lovejoy (1975) and others.

Cuvier's correct interpretation of *Pterodactylus* as a flying reptile is well-known among biologists. Less known is a footnote on this discussion which touches the question of the functional focus of other interesting organisms: flying and pseudo-flying fishes. Curiously, even after Cuvier's interpretation, the picture of an aquatic *Pterodactylus* with oversized flippers instead of wings persisted among some contemporaneous naturalists. For example, in a German commented translation of Cuvier's *Le Règne animal*, the translator August Vollrath Streubel "corrected" Cuvier's reconstruction in a footnote, referring to the work of other authorities (Louis Agassiz and Johan Wagler, among others). In Streubel's view *Pterodactylus* was an aquatic, not flying organism, and it could – at most – flap their wings in a way similar to flying fishes, such as *Exocoetus* and *Dactyloptera* (Streubel in Cuvier 1846, 631). The mentioning of Dactylopteridae as "flying fishes" is an interesting example of an interpretation of the functionality of features induced by intuitive but superficial and incorrect analogies. As the trivial name suggests, flying gurnards had been since long described and depicted in popular (Bertuch 1807; Hildebrandt 1911) and scientific (Abel 1912, 313-314; Agassiz et al. 1855, 56; Brehm 1883, 235; Hanstein 1929, 42; Lull 1927 (first ed. 1917), 356-357) publications of 19th and early 20th as able to fly. However, their pectoral fins are certainly not used for this purpose – these species usually do not even approach the water surface, and use the pectoral fins in display or anti-predatory behaviour by gliding in water (Fossa & Nilsen 1993, 111). As flying gurnards (or "helmet gurnards") were never the focus of scientific discussion as *Pterodactylus*, illustrations of Dactylopteridae as able to fly still occasionally can be found in modern zoological textbooks[26] and museum's displays (personal observation); see also Dawkins (1996, 120-121), who also pointed out this common mistake in modern publications.

[25] The total morphological pattern was conceived as a warning against analyses which make inferences based on single organismic traits. Curiously, the general aspect of this warning – the biased analysis of organismic traits – apply to some of Cuvier's application of his principle.

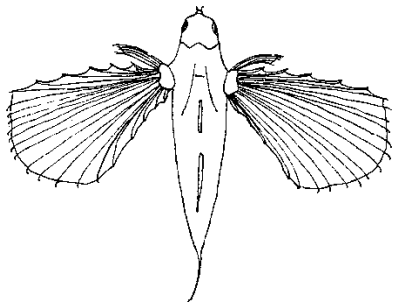
[26] See, e.g., Cloudsley-Thompson (1980, 186-187), who quoted Lull (1927) (see above). Lull did not speculate on this topic, as he quoted Moseley who wrote: "I have distinctly seen species of flying gurnets move their wings rapidly during their flight ... especially in the case of small species of *Dactylopterus* with beautifully colored wings, which inhabits the Sargasso Sea" (Moseley in Lull 1927, 356); see also below on Abel, who also believed an account of alleged flying *Dactylopterus*.

3.3.3 Discrepancies arising from wrong assumptions when compared with real diagnostic traits detected through a convergence approach

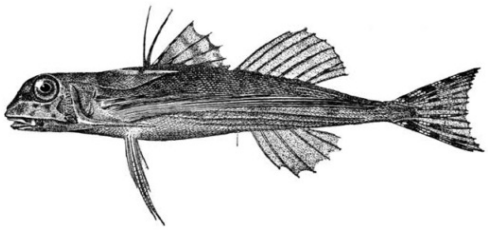
As shown in connection with the wrong assumption of Dactyloperidae as able to fly, our ability to detected patterns of functional similarity is not always accurate. As we saw, this mistake was also expressed by Othenio Abel. However, there is a fascinating aspect of Abel's wrong interpretation which makes this case clearly more interesting than the casual mistakes found in non-technical biological books written by non-specialists. Abel was certainly among the best specialists in the interpretation of functional traits in vertebrates in his time – several parts of his works are still highly interesting because of the quality of his analyses. Abel's mistake was not based on uncritical adoption of past misinterpretations: he trusted information delivered by Karl Moebius, a scientist of great reputation who claimed to have seen an exemplar of *Dactyloptena orientalis* flying on the edge of a coral reef southeast of Mauritius (Abel 1912, 317).[27] After Abel pointed out that flying fishes of the family Exocoetidae have – beside highly modified pectoral fins - an enlarged lower tail lobe[28] used to propel them out of the water, he was bewildered by the fact that in Dactylopteridae the upper and lower tail lobes are perfectly symmetrical. He was forced to conclude that an enlarged lower tail lobe could obviously not be used as a strong diagnostic trait for all flying-fishes (Abel 1931a, 206) – a wrong conclusion, as Dactylopteridae are not able to fly; see Fig. 3.2.

[27] I am assuming here that Moebius saw another species. However, as non-specialist on Dactylopteridae I cannot be conclusive on this point. All modern books written by specialists that I consulted refer to Dactylopteridae as not able to fly. The point here is that the references that I know on alleged flying Dactylopteridae is depicted in basic textbooks for undergraduates, without any reference to empirical evidence or on the possibility that Dactyloperidae are perhaps not able to fly. If it turns out that one or more species of this group can fly, the succinct statements on flying Dactyloperidae will nevertheless not be retrospectively "right" – analogous perhaps to the discovery of a real Yeti, which will not turn right all cryptozoological speculations on mythological creatures in the past.

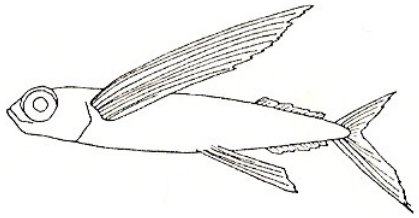
[28] In Abel's terminology: *hypobatische Schwanzflosse*, "hypobatic caudal fin".



A



B



C

Figure 3.2 Wrong interpretations concerning "flying fishes". Abel based his statement on Dactylopteridae as able to fly on a set of two traits: the enlarged pectoral fins (A) and the flying behaviour (based on Moebius' alleged observation); in this group the caudal fins are symmetrical (B) and therefore not consistent with the highly diagnostic trait "enlarged lower tail lobe" in other flying fishes (here: *Exocoetus sp.*) (C). Abel was aware of the contradiction between the alleged highly specialized flying behaviour of Dactylopeteridae and the symmetrical tail lobes. However, he was not prepared to regard the relationship between the form of caudal fins from (real) flying fishes and the function of accelerating the fish out of the water as a fantasy (*Hirngespinste*), and remarked that further investigations are still needed to clarify the issue (Abel 1931a, 206). (A) after (Lull 1927), also published in (Cloudsley-Thompson 1980); (B) after (Evermann and Marsh 1900); (C) after (Böker 1935). (Figures not to scale.)

Such details based on analogical inference of diagnostic traits identified in extant organisms are crucial in attempts to interpret functionality of traits found in fossil species. Abel's statement reveals a further aspect of the convergence approach: the importance of being skeptical about unproved assumptions at all stages of investigation, and to seriously consider aspects of the research which seem to contradict the adopted premises.

One of the ways to detect assumptions which can negatively influence adaptive analyses is to use historical investigations. Several examples of the use of weak or wrong assumptions in hypotheses used to contextualize early hominin evolution are analyzed in Appendix D; parts of this investigation was published in (Bender *et al.* 2012). As was shown there, several influential ideas on early hominin evolution in an open or semi-open environment, on the effect of climatic change in human evolution and on the use of analogies to discuss important

events in human evolution were uncritically adopted from hypotheses already proposed in the 19th century and early 20th century. It is argued here that the most influential of these hypotheses (known as the savannah hypotheses) were widely disseminated before the discovery of fossil evidence in South Africa in 1924 and its description in 1925 – an historical event often wrongly regarded as the beginning of the savannah hypotheses. Furthermore, the strong focus on the savannah hypotheses for decades and the negligence of alternatives could probably have been prevented by a general awareness that the fossil evidence discovered in Africa was interpreted in the light of the already popular savannah hypotheses. It is argued here that an awareness on the historical roots of the savannah hypotheses would motivate questioning the premises of this group of hypotheses and improve evaluation of the "biological plausibility" of scenarios on human evolution, as shown in the following chapter.

3.4 The concepts of biological plausibility and biological constellation

A further aspect of the convergence approach is related to the here proposed concepts of "biological plausibility" and "biological constellation" in the interpretation of adaptive features. To explain these concepts it is best to start with an example of early and modern speculations on the alleged role of apes' air sacs as floating organs, which is characterized by a large number of methodological flaws.

3.4.1 Biological plausibility concerning ideas on air sacs

Air sac is the term used to describe large cavities that are extensions of the larynx or other parts of the vocal tract found in many primates. They occur in most hominoids, but are absent in humans and smaller gibbons (Hewitt et al. 2002). Hewitt and co-workers investigated the possible function of laryngeal air sacs in hominoids. They pointed to the lack of evidence concerning this topic:

> These [air sacs] vary in size and configuration in different primate taxa. Only the large sacs of the apes, howler monkeys and cercopithecines are reasonably well known, while the air sacs in most other species of primates have not been a major area of research. A maximum of four types of air sac (lateral ventricular, subhyoid, infraglottal and dorsal) have been identified, but no single source describes the morphology and summarises the distribution of all the types of air sac. (Hewitt *et al.* 2002, 70)

They stated that the function of the different types of air sac remains uncertain, though most hypotheses on their emergence and functionality assume that these structures modify vocalisations (see Fick 1895; Fitch 2000; Gautier 1971; Groves 1972 and references therein for different hypotheses; Hewitt et al. 2002; Starck & Schneider 1960).

Some early authors ignored the interpretations of airs sacs concerning vocalization and became fascinated by the idea that air sacs can function as floating aids. These ideas are not motivated by aquatic habits of hominoids – most hominoids avoid large bodies of water – but they were probably formulated having in mind an implicit analogy between airs sacs in apes and personal floating devices (formed as inflated bladders of animal skins or other artificial aids) used by humans. In the first half of the 19th century, Georg Bennett read in an American publication (without giving further details) that air sacs in Siamangs might aid swimming. In 1834, he described the air sacs in a siamang (*Symphalangus syndactylus*), pointing out that this individual inflated his air sac when angry, vocalizing or yawning (Bennett 1834, 150-152). In an attempt to test the role of air-sacs as floating organs, he placed this individual in a water tub. Contrary to the speculations of the American publication, the animal panicked in water and submerged several times without ever inflating his air sacs (see chapter 4.3.3 on similar early tests of swimming ability in gibbons).

The idea of air sacs in apes having the function of floating devices, although naïve, seems to be an intuitive one, and different statements on this topic appeared in early publications, some implying an amazing degree of ingenuity concerning elementary physical concepts. For example, Vrolik[29] speculated on the possibility that air sacs in orangutans were used as a kind of swim bladders for "swimming in the air"! In a paper on body volume and air sacs of an adult orangutan, R. Fick aptly recognized the obvious flaw of Vrolik's ideas and wrote about a possible advantage of air sacs as floating devices *in water*:

> The air sacs would only provide a real mechanical advantage to the orangutan in water while swimming. But this is a case that certainly only very rarely or never occurs, because the orangutan is known to be very afraid of water and never or hardly ever leaves the trees. Moreover, the "neck-floating bubble" [Halsschwimmblase] would probably require a very inappropriate position of the body in the water and would force the orangutan to continuous "water treading". (Fick 1929, 78, my translation)

Several years later, in a remarkable example of convergences of ideas, the topic air sacs was enthusiastically adopted by some proponents of a modified version of the classical aquatic hypotheses and debated in internet forums.[30] As shown elsewhere, in the classical aquatic hypotheses it is argued that the ability of modern humans to swim and dive began to develop

[29] Mentioned by Fick (1929). Fick referred in the text to "Vrolik (1795)", but he forgot to give the reference in the reference list. If Fick meant the Dutch anatomist Willem Vrolik (1801-1863), then the year "1795" is a typo. I still have to find Vrolik's original publication on airs sacs to confirm Fick's information.

[30] For different opinions on this topic see https://groups.yahoo.com/neo/groups/AAT/info and http://www.aquaticape.org/

around the time when early hominins developed permanent bipedalism. In the modified version it was the *ancestors* of nonhuman hominoids who developed aquatic features. Without awareness of early predecessors in these analogies, the proponents of this scenario argue that air sacs in apes evolved as a floating organ to keep the head above the surface, convergent to air-filled structures such as vocal sacs of frogs, swim bladders of bony fishes or gas-filled chambers in nautiluses allowing slow swimming or floating; they assume also that tail lost is a consequence of this aquatic past. As apes evidently do not show any sign of aquatic features, it is assumed that they lost this ability in the course of their phylogeny, and air sacs in apes are relics of this aquarboreal past.

The air sacs-analogies from the 19th century and modern publications are used here as examples of unsubstantiated speculation with respect to water use and as a starting point for the definitions of the concepts of biological implausibility and biological constellation.

Biological implausibility refers to the *inferences based on weak thought experiments or comparisons between distantly related organisms bearing superficial similarity in traits without considering data on functionality and evidence based hypotheses on the emergence of these traits.*

Not all possible scenarios for the evaluation of functionality of traits are worth being included in the scientific debate. Although single hypotheses can be absolutely rejected because they are based on physically impossible events – as the above mentioned speculation on air sacs in orangutans with the function of "swimming in the air" – these cases are exceptional. Most weak hypotheses can be regarded as theoretically possible, but are nevertheless highly implausible, as shown here for the air-sac analogy:

(a) This scenario is strongly weakened through the previously exposed arguments by R. Fick of orangutans being reluctant to enter water; the argument of extant apes as once semi-aquatic is an assumption that contradicts evidence on water use in extant nonhuman hominoids (see below, chapter 4.3 on data on this topic). In fact, it is difficult to imagine a mammal taxon less suited as candidate for such an ex-aquatic scenario than hominoids.

(B) Several authors working with empirical data suggest vocalization as a main factor in the evolution of air sacs in primates. The suggestion of major functional changes (air sacs as floating organs subsequently changed to perform other functions, among others vocalization) lacks any empirical basis.

(C) Vocal sacs in frogs is part of the structure of the mechanism of sound production in frogs (Duellman & Trueb 1986, 89-107). There is no empirical evidence of these structures had once been used as "floating organs" in the past, as implied in the comparison of aquarborealists.

The term "biological constellations" are used here to describe *the product of methodologically unsound selection of traits to corroborate a preconceived scenario on the evolution of these traits*. I borrow the term constellation from modern astronomy, where it is defined as "any of a number of apparent groupings of stars in the form of imaginary configurations in the sky" (*Encyclopedia Americana* 1977, 7th volume, p. 654). The implication of "imaginary configurations" applies very well to the here proposed concept. For instance, the attempt to use traits like airs sacs in frogs and apes, tail lost in frogs, sloths and hominoids as part of the same comparison in an attempt to corroborate a preconceived hypothesis on human evolution is an example of biological constellation: the functional interpretations from the single features are already erroneous, so that merging these different traits into a unified scenario is additionally misleading. The pattern emerging from this chunk of traits is unreal. As shown in the next section, the tendency to use biological constellations is detectable both in classical as well as alternative scenarios on early hominin evolution.

3.4.2 Biological constellations in the savannah and aquatic hypotheses

A full analysis of the emergence and development of the traditional hypotheses presented to contextualize early hominin evolution is provided in Appendix D. This mostly historical analysis is an integral part of the work; it is not placed here, because it would disrupt the flow of the present chapter. In summary, the emergence of the early ancestors of human beings is traditionally explained in connection with the "savannah hypothesis". 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. In the 19th century and especially in the first third of the 20th century several works were published in different European languages in which analogies between humans and vertebrates adapted to an open environment were intrinsic parts of the argumentation; analogies are still influential in palaeoanthropological research (see Tables 6.2-6.5 and Appendix D). In recent years – as a continuation of the development that took place in the early 1960s forward – several 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.

The analysis presented in Appendix D shows that there is no clear line between the savannah hypotheses and the alternative scenarios in the use of analogies to corroborate alleged adaptations of hominins to different environmental settings. The similarities in the methodological flaws were – as far as I can judge – never acknowledged in the literature. One of the reasons for this is the tendency of critics of the alternative hypotheses to defend the classical ideas, ignoring similar methodological flaws in their own hypotheses. The same applies to the proponents of the alternative ideas, who tend to see the savannah hypotheses as a counterpart to their own ideas. However, in both groups of hypotheses a high degree of oversimplification, biological constellation and sometimes biological implausibility can be detected (for a further discussion on the similarities between the aquatic and savannah hypotheses see Appendix D).

Several examples of a poor use of convergence as a tool in primatology and palaeoanthropology refer to the lack of methodology in hypotheses proposed for alleged aquatic features in different primates, including humans. Several of these speculations were proposed in the early 20th century or earlier. For instance, Herbert F. Standing speculated on the extinct lemur *Palaeopropithecus* as an aquatic animal adapted to swim at the water surface (Standing 1903).[31] Inspired by Standing, the Italian palaeontologist G. L. Sera developed further the idea of *Palaeopropithecus* as an aquatic-arboreal organism, applying the same idea to interpret several other primates as aquatic or descending from aquatic organisms (Sera 1935; Sera 1936; Sera 1938); see discussion in Bender-Oser (2004, 91-96); Sera's aquatic hypotheses were criticized by Charles Lamberton (1957); on early and modern interpretations of *Palaeopropithecus* see Godfrey and Jungers (2003).

In the 1930s the director of the Dermatological University Clinic in Prague, Franz (or František) Šamberger published an article where he pointed to specific dermatological traits in

[31] In following statement Standing interpreted several osteologic fossil traits of Palaeopropithecus as aquatic adaptations:

> Tous ces caractères sembleraient nous indiquer qu'il s'agit ici d'une spécialisation très remarquable, et je ne crois pas me tromper en pensant que plusieurs de ces caractères ont été acquis par les membres de ce groupe en s'adaptant à une vie aquatique. En effet, une ligne menée par les orifices des trois principaux organes des sens: le nez, les yeux et les oreilles, est droite et normale au plan de l'occiput. L'animal, en nageant à fleur d'eau, a dû être obligé de tenir la tête dans une direction horizontale suivant la surface de l'eau, ce qui nous expliquerait la direction horizontale prise par cette ligne. De plus, le corps a dû continuer cette même direction qui concorde exactement avec la direction de l'occiput dont les condyles sont aussi tout à fait verticaux. (Standing 1903, 235)

humans to speculate on a possible "amphibious phase" in human evolution (Šamberger 1933a). Similarly, in 1909 Bruno Henneberg interpreted traits in the human ear as possible relics of an aquatic adaptation; more than 30 years later he published a further article on this topic (Henneberg 1942); the German pathologist Max Westenhöfer, based on different anatomical traits (and referring to the above mentioned works by Sera, Šamberger, Henneberg and others) developed the first extensive scenario on humans developing several traits in response to an aquatic environment (Westenhöfer 1923; 1935; 1942); for an historical analysis of "aquatic hypotheses" see Bender-Oser (2004); for a summary of Westenhöfer's ideas see Appendix F.

Westenhöfer's aquatic hypotheses would be only of historical interest (he was anti-Darwinist and defended other eccentric ideas on human evolution, see Appendix F), if his *aquatile Hypothese* would not have been re-discovered or independently formulated by Alister Hardy and become through the publications by Elaine Morgan, an important counterpart to the classical savannah hypotheses (see Appendix D). I would like to discuss here some methodological problems related to the aquatic hypotheses arguments and to the criticism of these ideas.

A general problem with early and modern aquatic hypotheses concerns what seems to be a high degree of biological implausibility implied in different arguments. For example, Max Westenhöfer and later Elaine Morgan argued that ventro-ventral mating position evolved in humans convergently in aquatic and semi-aquatic mammals, like dolphins or beavers (Morgan 1972, 62-63; Westenhöfer 1942, 311-312). This attempt to explain the emergence of human traits by referring to highly adapted aquatic organisms evokes logically the picture of human ancestors being as highly adapted to an aquatic life as dolphins and beavers. In fact, most critics of the aquatic hypotheses evaluated the different arguments with a similar logic: as humans are obviously not highly adapted to an aquatic environment (when compared to dolphins and beavers) and since it is not parsimonious to state that they were more aquatic in the past, we have to conclude that the aquatic hypotheses are wrong. Taking the example of the mating behaviour, it seems plausible to argue that face-to-face mating[32] in aquatic mammals is related to their highly specialized morphological adaptations and to the difficulty to copulate without contact with a solid substrate. The idea of early hominins swimming and (at the same time!) copulating in water in a dolphin fashion is biologically highly improbable or physically impossible.

[32] Face-to-face mating in cetaceans is described in most books on the subject; mating face-to-face in beavers is described in Krumbiegel (1929) and Mertens (1928).

The problem is that most proponents of the aquatic scenario compared humans with highly specialized aquatic organisms without *implying* that humans were also similarly highly aquatic. For example, in a paper on the evolution of nakedness in *Homo sapiens*, Rantala summarized the main arguments of the aquatic hypotheses and concluded the passage as follows: "It is not very realistic to claim that humans have ever lived such a totally aquatic life as those marine mammals that have shed their fur. It is more likely that our ancestors lived on the shore and caught their food offshore by wading and diving. Humans would naturally have returned to the beach to sleep, and would have spent most of their time ashore" (Rantala 2007, 4). Rantala understood the arguments "early hominins lost the hair in a semi-aquatic environment" and "humans have a naked skin like dolphins" as an indication that early hominins lived completely aquatic. This of course is wrong (see details in Appendix D, chapter D.6.3): proponents of the aquatic hypotheses (Hardy 1960a; 1960b; 1977; Morgan 1972; 1982; 1990; 1997; 2008) or of versions of the aquatic hypotheses (Kuliukas 2011a; Kuliukas & Morgan 2011; Niemitz 2002; 2004; 2010; Verhaegen 1985; 1997) did not defend the idea of early hominins fully adapted to an aquatic life. A careful reading of the ideas expressed by Alister Hardy and Elaine Morgan reveals that several arguments were formulated with the implicit assumption of early hominins able to swim and dive with the same degree of proficiency as observed in modern humans. For example, Morgan did not mention in any of her publications that hominins once copulated in water like dolphins. She rather implied in her arguments that early hominins mated ventro-ventrally on land due to constraints related to morphological adaptations to water, like a streamlined body form, ventralization of the vagina and the development of steatopygia in hominin females (Morgan 1972, 60-66). This more subtle way of argumentation was mostly not considered in the criticism expressed against the aquatic hypotheses, as most critics were not careful enough to study the nuances of the arguments, or were interested in overlooking these nuances in order to easily falsify the arguments. My falsification of the ventro-ventral hypothesis proposed by Westenhöfer and Morgan follows: not only humans, but also other apes copulate regularly or sporadically face-to-face, for example, bonobos, orangutans and gorillas.[33] This indicates that ventro-ventral copulation is part of the versatile hominoid mating behaviour that renders obsolete the argument of an alleged convergence between hominins and aquatic animals with regard to this specific trait.

[33] Interestingly, Morgan was aware of the face-to-face mating in orangutans and gorillas, but she preferred to interpret this trait in a convergence approach (Morgan 1972, 62-63).

In the next section a specific hypothesis proposed to contextualize early hominin evolution in connection with thermoregulation is analysed. This case was chosen because it is an influential model and characterized by a lack of analogies and a high degree of oversimplification.

3.4.3 The sun-streamlined hypothesis

One example, among many, of the use of oversimplified landscapes in hypotheses on early hominin evolution can be identified in the different articles published by Peter Wheeler in the *Journal of Human Evolution* from 1984 onwards. I am choosing Wheeler's ideas as a negative example. However, although his ideas are here considered as based on weak arguments, Wheeler is one of the few scientists considering topics often neglected in palaeoanthropology, like thermoregulation and soft tissue, and I regard these efforts as highly welcome.

In his "sun-streamlined hypothesis" (my name for it) Wheeler assumed that the evolution of hominin naked skin and bipedalism took place in open plains. These assumptions are explicitly stated in different parts of the paper, as in following sentences: "The early hominids are thought to have inhabited the African equatorial savannahs, environments where the high levels of direct solar radiation cause considerable thermal stress" (Wheeler 1984, 92). After stating that in modern man heatstroke "can result from elevations in core temperature of less than 4 °C" he continued: "Therefore one of the principal adaptations required by these primates to exploit fully the more open savannah environments would have been an extremely effective whole-body cooling system" (Wheeler 1984, 92). On the other hand, he assumed that as "a direct consequence of a naked skin man has the most effective body cooling system of any living mammal" (Wheeler 1984, 91). Based on these assumptions, and pointing to the fact that naked skin is not a typical trait for savannah mammals, he suggested a hypothesis in which hominin bipedalism combined with relative hairlessness and larger body size resulted in a major thermoregulatory advantage when compared with the thermoregulatory systems of quadrupedal savannah mammals. A hominin, so Wheeler, experiences a much lower radiant heat load through a biped posture when walking in open plains at noon, e.g., at a time the sun is near its zenith. In the following analysis we will focus on some specific arguments of his extensive theoretical model. Further comments on Wheeler's ideas were published by other authors (Amaral 1996; Chaplin et al. 1994; Dean 1990; Porter 1993); see also Wheeler's reply to this (1994b; 1996).

Thermoregulation is very important both for homeotherm and poikilotherm animals, since several biological processes perform optimally within a narrow range of temperature; animals can be damaged or killed by exposure to very high or low temperatures. For this reason, most animals show specific strategies to avoid extreme temperatures through a flexible behaviour, as demonstrated in several taxa (Bennett et al. 1984; Bicca-Marques & Calegaro-Marques 1998; Heinrich 1999; Kemp & Krochenberger 2002; Maloney et al. 2005; May 1976; McNab 1970; O'Neill & Rolston 2007; Paterson 1981; Robinson & Robinson 1974; Seebacher 1999; Whiteman & Buschhaus 2003). Many terrestrial animals move to sunny places in the morning or later afternoon and to shadowed places (or in some cases to water) during the hot hours.

One important aspect of Wheeler's hypothesis concerns the lack of comparative data to corroborate it. As we will see in the guideline (3) of the convergence approach (chapter 3.6), it is important to show comparative data even in cases where it is assumed that an organism is unique concerning a certain feature. For example, Wheeler could try to demonstrate cases in which organisms show at least sporadic events of upright stance in open plains as a response to thermal stress, or discuss the absence of convergences. Comparative data would add a strong evidence based argument in his theoretical construct. The reason why Wheeler did not use such data is probably related to the fact that such behaviour is unknown: to my knowledge, there is no empirical data or even anecdotal observation on non-human primates or any other vertebrate regularly standing or walking upright in open plains at a time when the sun is near its zenith as a specific response to thermal stress. As stated above, primates (including humans) and other mammals usually seek for shadow in the period around midday; the patas monkey (*Erythrocebus patas*), a fairly common species in the savannah and woodland savannah in Africa, is not an exception to this rule: he rests during the hottest hours (Hall 1965; Hall et al. 1965). Even species showing specific adaptations to protect themselves against the sun in hot arid regions avoid the open plains at midday. For example, the Cape ground squirrel (*Xerus inaurs*) uses its bushy and long tail as a portable parasol to shade the body (personal observation). This conspicuous behaviour was described and quantified by Bennett and colleagues. The squirrels turn their backs to the sun wherever temperature exceeds approximately 40° C. By using this strategy, the squirrels are able to extend greatly their periods of continuous surface foraging. Nevertheless, the adaptation has limitations: at midday, the animals frequently retreat to their burrows (Bennett *et al.* 1984).

I am not aware on any hypothesis formulated to explain permanent bipedal posture in other organisms (extinct or extant) with similar arguments as those proposed by Wheeler. It is

useful therefore to consider behavioural features related to heat management in other organisms in order to evaluate the sun-streamlined hypothesis from the perspective of a convergence approach. One interesting example refers to the adaptations of dragonflies (Odonata). In the 19th century it was observed that dragonflies sometimes adopt a very peculiar posture, the so-called obelisk posture, in which the abdomen is pointed vertically toward the sun - or nearly vertically, depending on the orientation of the perch (Gonzáles-Soriano 1987) (Fig. 3.3).

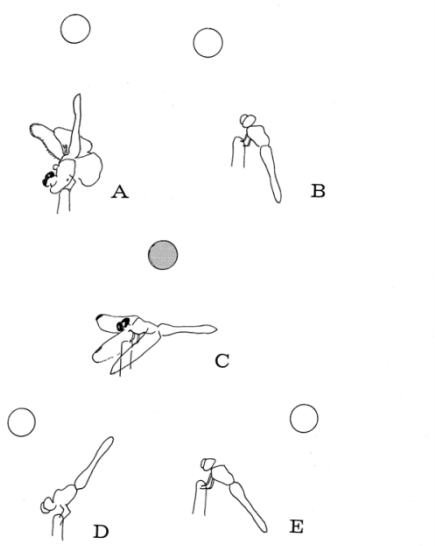


Figure 3.3 Obelisk posture in dragonflies. Postures in Libellulidae that minimize (a and b) and maximize (c-e) exposure to the sun. Stippling indicates sun above or behind the plane of paper. This thermoregulatory behaviour has a low constraining effect (because it is flexible) and a low cost (modified from May 1976).

Corbet (1962, 130) hypothesised that in certain tropical species, the obelisk posture might be used for a thermoregulatory function by minimizing the surface area exposed to radiant energy. Hardy (1966) showed that in *Perithemis tenera* the posture relative to the sun is correlated with air temperature. May (1976) was the first author to note how many dragonflies thermoregulate, examining the range of behavioural and physiological adaptations that make this possible. He showed that through the obelisk posture, the body's shadow is reduced by more than 50 per cent; this posture probably serves for ectothermic cooling and is observable in ca. 30 species of dragonflies (May 1978). When the sun is close to the horizon, a vertical posture can be assumed for the opposite purpose (Dell' Anna et al. 1990). The obelisk posture is adopted by typical "perchers." Perchers are typical heliotherms, changing different postures

depending on ambient temperature. Fliers, in opposition, fly continuously; some of them are endothermic regulators during flight (see also a recent review in Corbet 2004, 282-294; May 1976).

If we compare the thermoregulatory adaptations of the dragonflies and the hypothetical adaptations of early hominins proposed by Wheeler, we find some crucial differences. In dragonflies, the adaptations can be observed constantly in many species living today relative to a specific range of environments – real environments. The obelisk posture is part of a flexible behavioural pattern being effectively used in clear connection to the changing position of the sun. The thermoregulatory behaviour of the dragonflies is compatible with the assumption that a flexible thermoregulation is advantageous, as long as the cost of regulation is not too high. In opposition, Wheeler's hypothesis is based on a thermoregulatory behaviour that cannot be observed in modern humans. In his hypothesis, Wheeler ignores the essential fact that humans (like most mammals) avoid being exposed to direct solar radiation at noon in a tropical environment. Many human cultures inhabiting hot climates take a prolonged lunch break in order to avoid the highest temperatures of the day (Parsons 2003, 44-46; Walter 1974, 88). Wheeler avoids in his publications the difficulties related to the origin of such a committing trait like permanent bipedalism to forage in highly limited temporal/geographical dimensions. In fact, any deviations of the postural, temporal and geographical conditions (for instance, hominins changing posture during foraging behaviour) would compromise the validity of his mathematical models. Wheeler and several critics of the sun streamlined hypotheses did not realize that this model implies a stationary permanent biped hominin – a highly improbable situation for a real organism living in a real environment. Other authors (Ruxton & Wilkinson 2011a; Ruxton & Wilkinson 2011b) modified the sun streamlined hypothesis to represent a walking / running hominin rather than the stationary form considered by Wheeler; these authors believe that hair loss, but not bipedalism evolved for thermoregulatory reasons.

In the literature on behavioural and physiological thermoregulation, there are no examples of savannah mammals showing such static and constrained adaptations. Thermoregulatory behaviour known in mammals and birds (examples in herring gulls: Luskick et al. 1978; in wildebeest: Maloney et al. 2005; in primates: Paterson 1981) is generally connected with low-cost and low-constraining orientation of the body relative to incident solar radiation and wind, sometimes associated with some specific anatomical and physiological adaptations. The slow and probably energetically inefficient bipedalism of early hominins would have been an even

more improbable adaptation to an open and hot environment that emphasizes the biological implausibility of Wheeler's hypothesis. The expression "energetically inefficient bipedalism" refers to the theoretical consideration (see chapter 6 for discussion of fossil evidence and references on this topic) that the incipient early hominin bipedalism was on the one hand energetically less efficient than the locomotory pattern of early hominin ancestors (which probably showed only sporadic terrestrial bipedalism); on the other hand it refers to the energetically less efficient locomotory pattern when compared with the more optimized bipedalism in more recent hominins.

Another example of a structure specifically designed for thermoregulatory purposes through orientation to the sun is the nest of compass termites (*Amitermes meridionalis*) on the Australian steppe of the Northern Territory (see Fig. 3.4). Their broad sides face east and west, and their short sides face north and south. Through this solar alignment, the weak morning sun delivers some heat to the structure (without any danger of overheating the broad side of the nest), and during the time the sun approaches the zenith, the incidence of solar radiation is considerably avoided, since it will fall on the short side of the structure. The nest of the compass termites (in contrast to the early hominins in Wheeler's model), does not have to be closely placed to the equator to be effective. Similarly, this structure does not have a restricted advantage at noon. In contrast to Wheeler's early hominins, the termites' nest has no choice other than to "behave" statically in its environment. Their thermoregulatory flexibility is improved by other behaviour: termites can move inside the nest, reacting to the temperature differences within the towering structure (see Korb 2003).

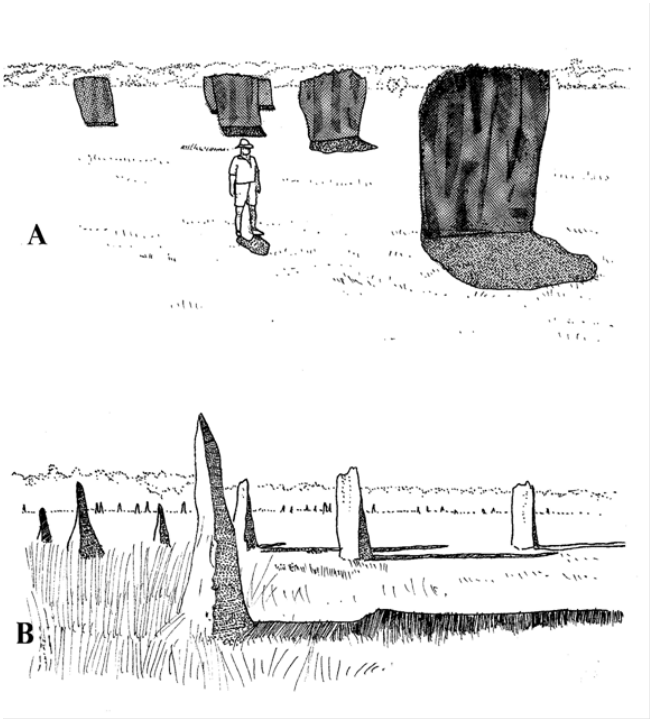


Figure 3.4 The nest of compass termites (*Amitermes meridionalis*) on the steppes of Australia is an impressive towering structure, which may be up to five meters high and three meters long. Their broad sides face east and west, being exposed to the weak morning sun (a), their short sides face north and south, exposing less surface to the sun approaching the zenith (b). More explanations are in the text. (Drawings after photos in Frisch 1974)

The assumption of such singular and highly constraining thermoregulatory features of early hominins (as assumed in Wheeler's model) reflect the attempt to integrate some hominin features into the framework of a classical savannah hypothesis. This integration is only possible using an oversimplification of the theoretical model and a disregard of the conditions present in real environments and convergent solutions evolved by other mammals living in the same environment. Such oversimplifications can also be found in other savannah and aquatic hypotheses (see Appendix D). Most of them assume unique adaptations for different features of early hominins, ignoring that without the necessary corroboration using convergences, almost every imaginable hypothesis conceptualizing hominin evolution is possible, as long as the difficulties implied in these models are ignored. In fact, the verification of models that assume unique features in early hominins is almost impossible without the use of comparative data – and exactly this is excluded by assuming hominins as unique.

Another insightful aspect of Wheeler's sun-streamlined hypotheses is the fact that in later publications Wheeler changed his original model (Wheeler 1993; 1994c). In the amended version he proposed that early hominins were shadow-seeking at noon like other savannah

mammals, noting that this behaviour is even more effective in reducing heat load (Wheeler 1994c). Wheeler did not make transparent the resulting contradictions with the original version. In fact, in this new model hominins are behaving in a similar way as extant savannah organisms and modern humans in hot, arid environments. We can only speculate what motivated Wheeler to change his model. One possibility is that these changes were conceived to accommodate the doubts expressed towards the savannah hypotheses and the increasingly emphasis of a mosaic environment in the scenarios proposed to contextualize early hominin evolution in early 1990s. I am not criticizing Wheeler for changing his ideas. In fact, his shadow-seeking hypothesis is in my opinion superior to his sun-streamlined hypothesis. (To be sure: Wheeler's second hypothesis is also weak, as seeking shadow *is* the usual behavioural patterns in mammals adapted to open savannah and therefore, logically unsuited to promote a hypothesis on an alleged superior ability to thermoregulate in humans.) However, Wheeler missed the opportunity to point out the discrepancies of his ideas. The lack of inner logic in his hypotheses was scarcely noted, so that his papers (the pre-1994 and the 1994 paper) are often quoted as part of the same theoretical concept.

3.5 Establishing groups of comparison in the convergence approach

Although the general idea of an extensive consistency in the relationship between traits and environment is crucial in functional analyses, our ability to interpret functional relationships is limited. This applies not only to fossil material, but also in the attempts to predict performance of structures observed in extant organisms. For example, swimming ability is expected in most terrestrial vertebrates (see chapter 4.2.6) even in species in which the anatomy seems to be incompatible with this behaviour (like in bats). Some authors assumed that some species are not able to swim because of certain traits, such as small amount of body fat in non-human hominoids (see chapter 6.8.1). However, the loss of buoyancy due to specific anatomical traits like armor shell, heavy structures placed on the head or less body fat can be compensated for in part by different strategies – for example, by inflating the stomach with air or simply by more efficient or vigorous swimming movements. These and other strategies make it difficult to predict only from the anatomy of a terrestrial vertebrate the distance it can cover by swimming. The data presented in the review of chapter 4.2.6 suggests that poor swimming ability should be expected in terrestrial vertebrates with heavy antlers or horns, or animals with strong adaptations to an arboreal life. This prediction, however, is only valid for animals with a long evolutionary history of absent or irregular interaction with large bodies of water – information which cannot be inferred easily from fossil evidence. The difficulty in inferring swimming ability from anatomy is simply illustrated: several humans

(see chapter 5.4.3) and most extant non-human hominoids (see chapter 4.3) are unable to swim; their inability to swim cannot be inferred from their anatomy, which does not differ from the anatomy of several humans and the few non-human hominoids able to swim; see also chapter 3.1 an example of aquatic birds (dippers) without easily recognizable adaptive aquatic features.

We saw several negative examples of the use of comparisons between distantly related species from the point of view of convergences and we saw some common problems related to the lack of a method in these comparisons. In fact, it is surprising that methodological aspects of how to compare distantly related species have not been discussed in depth in the literature. This lack of methodology is because several convergences are clear - we do not need a formalized method to recognize that the fast-swimming fusiform morphologies found in different tetrapod vertebrates (like dolphins and ichthyosaurs) are obviously similar and intrinsically related to fast swimming. However, several human traits like reduced hair cover and permanent bipedalism cannot be directly compared with similar traits found in other organisms – we do not have other hairless permanent bipedal mammals living today. In fact, we do not know even when in human phylogeny the hair cover began to be reduced and we still do not know (contrary to the opinion expressed in some biological textbooks) under which specific selective pressures permanent bipedalism evolved in early hominins. The fact that several key human features were compared unsystematically with distantly related species reaching contradictory conclusions concerning the adaptive value of bipedalism and hairlessness in humans is a strong indication that a convergence approach formalized methodology for these comparisons is urgently needed; see Tables 6.2-6.5 for an overview of these hypotheses.

Here such a convergence approach for the comparison between distantly related groups is proposed. The aim is to supply criteria for the formation of groups / traits to be compared, and guidelines for practical steps needed for the inferences from such comparisons. First, an example on how to use the concept of functional focus in the convergence approach is presented.

Pangolins (Pholidota), anteaters (Myrmecophagidae), aardvark (*Orycteropus afer*), numbat (*Myrmecobius fasciatus*) and other mammals show a set of highly diagnostic traits associated to feeding on ants or termites, as a long, thin and highly extensible sticky tongue, strong curved claws, reduction or loss of teeth and well-developed olfaction. These traits were developed more or less independently in these species (Reiss 2000). The interpretation of

these structures as myrmecophagous adaptations is not controversial. However, despite the clear adaptive traits in this group, myrmecophagous mammals can use the specialized structures and behaviours for feeding on other items. For example, as described by L. S. B. Leakey, giant pangolins (*Manis gigantea*) were observed feeding on water beetles:

> Wading into the shallow water of the swamp or into a reedy backwater until it is far enough immersed for its lips to be level with the water surface, the pangolin puts out its long, flat, tape-shaped tongue and "woggles" – there is no other word – it over the surface of the water. Attracted by this moving object (a similar situation can be simulated by moving a stick over the water), the water beetles come swarming in from all directions. As each, in turn, comes into contact with the pangolin's sticky tongue, it is sucked into the mouth and swallowed. (Leakey 1974, 32)

Leakey dissected a pangolin and found that the total content of its stomach was "a mass of water beetles" (Leakey 1974, 32). It seems difficult, based only on this evidence, to infer a past selective pressure for feeding on water beetles. By assuming that the trait "long sticky tongue" is convergent to the similar trait in the other species mentioned above I do not assume to know all cases of functional changes, presence or lack of constraints and selective pressures in the emergence or modification of the tongue in this species. The same applies to other traits associated to feeding on ants and termites, as the strong curved claws, which are also used in other species for completely different biological roles, as for instance by the extant sloths (in the context of arboreal environment) and extinct sloths, which include among others also large terrestrial species with strong, curved claws (Coombs 1983).

On the other hand, there are several other species eating ants and/or termites which do not show the same degree of specialization of the species above (Redford 1987). For instance, common chimpanzees (*Pan troglodytes*) use long and rigid twigs or sticks to extract not only termites, but also ants from terrestrial nests. Their tool-use repertoire is far from species typical (McGrew 1996) and they do not show any visible morphological or physiological adaptation to this feeding technique. For example, they avoid painful ant bites by staying as far as possible away from the nests or by hanging from a nearby tree during the ant-dipping (McGrew 1977). Despite this rather poor performance when compared with specialized species feeding on ants, it is possible to compare common chimpanzees and these specialists, if the use of tools (long and rigid twigs or sticks) and the apparent lack of specific adaptations to ant-dipping are explicitly acknowledged in the comparison.

A large number of patterns of non-homologous similarities are found in prey-predators relations; see further explanations and references in chapter 6.6. This topic offers several insightful examples of convergences between organisms of different taxa, giving the opportunity to discuss methodological aspects on how to compare distantly related species in connection with predation.

In Fig. 3.5, we see distantly related species having different traits associated with similar hunting strategies. At first sight, it seems impossible to compare, for example, amphibians with insects. However, this comparison might be possible with clear definitions of the employed categorization. Some categorizations are obvious. One evident case of traits in several species of frogs (Anura) which can be regarded as convergent to traits of other groups refers to their ability to use long projectile tongues to prey on insects from a certain distance. Apart from frogs, the trait "long projectile tongue" developed convergently in several species of salamanders (Salamandridae, Hynobiidae and Plethodontidae) and in chameleons (Chamaeleonidae) to hunt in a similar way. The comparison between frogs, salamander and chameleons is only possible by considering the differences and similarities in this hunting strategy. The feeding mechanisms used in different tetrapod groups can show extreme variations in form and function, but the fact that they represent modifications of homologous parts make the comparison between frogs, salamanders and chameleons very interesting to comparative analysis (Schwenk 2000a). From this perspective, the research on the long tongue mechanisms used to prey on insects in these groups is more interesting than a comparison between these groups and, for instance, insects or fishes.

The establishment of comparative groups including frogs, insects and fishes are insightful for other reasons, as the comparison focuses on more general aspects of the relation between the species. For instance, the hunting strategy of the convergent groups of insects Mantispidae and praying mantis (Mantodea) can be described in great detail taking into consideration their physiology, morphology and behaviour, as they share a similar Bauplan. A comparison of these insects with frogs, salamanders and chameleons can be justified by pointing to at least one common element found in these groups, in this case: they use parts of the body to project at high speed onto the prey. This formulation allows searching for further traits that are associated with this hunting strategy, for example camouflage (if they are ambush predators) and the ability to stay perfectly still for long periods of time. This categorization can be further expanded by including not only parts of organisms, but also the acceleration of whole bodies in the hunting strategy, as in the case of Bengal tigers (*Panthera tigris tigris*), snakes

(Serpentes) and aquatic African dwarf frogs *(Hymenochirus).* A further expansion is possible by including tools in the hunting strategy, as used by archer fish (Toxotidae), which are known for their ability to prey on insects above the surface of the water by projecting spouts of water, and by humans, hunting with projectile weapons. In every new categorization, new aspects can be revealed by the comparison. For instance, the aspect of camouflage is not so important to the fishes' hunting by spitting water as for chameleons or praying mantis.

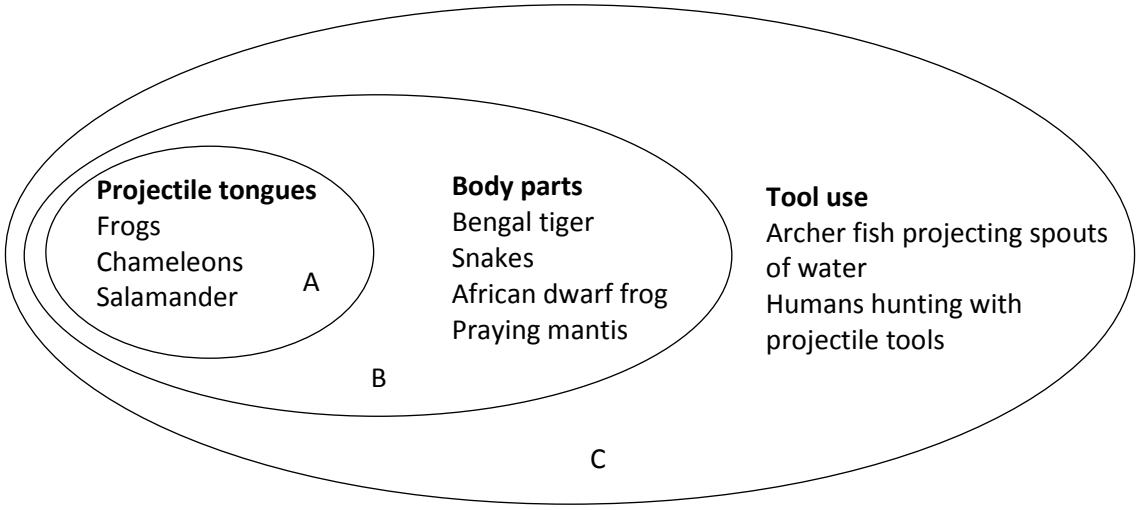


Figure 3.5 Example of comparison of distantly related organisms by using different categorizations of studied traits. A. Category including frogs, salamanders, and chameleons focusing on the trait "long projectile tongue" used to prey on insects. B. Expansion of A by including "non-tongue body parts" used for catching prey. C. Further expansion of B including the use of projectile tools for hunting. See further explanation in text.

Although the above examples are very simple, by following the convergence approach we can prevent the methodological flaws of hypotheses like the analogies between air sacs in primates and vocal sacs in frogs, or several comparisons early hominins and savannah animals (Appendix D) which are examples of biological constellations (unreal patterns of similarity). We can also use the example of preying strategies to demonstrate an obvious case of invalid comparison: the trait "long tongue" of frogs is not comparable with the "long tongue" of the myrmecophagous mammals discussed above. Frogs and pangolins feed on insects, but the difference in the feeding strategy and in the use of the tongues is evident. As we see, it is not only the superficial similarity between traits which is decisive for the comparisons: the tongue of pangolins is morphologically more similar to the tongue of frogs than the latter to the stick used by a chimpanzee to fish ants. However, functionally the stick used by the chimpanzee and the pangolin's tongue are analogous considering their function of feeding on ants.

The convergence approach is useful to search for common properties in the studied groups. The example of swimming in turtles illustrates how a more complex behavioural trait can be investigated with this method. Although several basic aspects related to the origin of the turtles (Chelonii) remain obscure, it is generally believed that all turtles descend from more aquatic species. The oldest known turtle is *Odontochelys semitestacea*, or "half-shelled turtle with teeth" from the late Triassic, which inhabited sea shores or river deltas (Li *et al.* 2008). The idea that early turtles evolved in a semi-aquatic environment is not based on observations showing that extant turtles are proficient swimmers, as extant species are adapted to very different environmental conditions. Although little has been published on the ability to swim in this group, anecdotal data suggests that at least some species adapted to a terrestrial environment have very divergent swimming performances. For instance, observations gathered in connection with operations carried out to rescue animals trapped on islands after the damming of rivers suggest that *Chelonoidis denticulata* are poor swimmers and prone to drowning (Walsh 1969, 60-61). However, caution should be exercised in this kind of inference: the tortoises found by Walsh were starving on an island formed by the flooding and the very weak animals drowned when trying to swim (Walsh 1969, 61), so we cannot know if the swimming ability of this species can be inferred from these weak animals. Additionally, the same species is described elsewhere as good swimmers (Bonin et al. 2006, 213). Here we are confronted with a basic difficulty in the assessment of swimming ability based on anecdotal data: in nature we do not have the controlled conditions of laboratories, and divergent environmental settings and differences in the physical conditions of the observed individuals are only some of the several factors which might be relevant in an objective evaluation of the studied behaviours. For this reason, anecdotal data must be considered including the largest number of observations available.

On internet forums it is sporadically stated that tortoises are prone to drown in captivity, without defining these specific settings. Succinct statements in scientific literature are often not conclusive for the reasons explained above. For instance, Davenport wrote that terrestrial tortoises' swimming ability "is usually very poor indeed" (Davenport et al. 1984, 447). Vanessa Montgomery (personal communication) confirms that desert tortoises (*Gopherus agassizii*) are not able to swim, giving a more detailed description of the specific behaviour towards water in this species: *G. agassizii* is able to walk on the bottom of a pool for a short time, but drowning usually occurs if it cannot reach land fast enough. Further terrestrial tortoises are reported as not being able to swim or as poor swimmers, like the star tortoise (*Geochelone elegans*) (De Silva *et al.* 2011), or the giant Galápagos tortoise (*Geochelone*

nigra), which however, were also described as able to float (Beheregaray *et al.* 2004; Caccone *et al.* 2002). As we saw in the hippopotamuses, the equation "semiaquatic species equals good swimmers" is not precise. Turtles adapted to an aquatic environment progress in water by using the forelimbs to swim, the hind limbs used for steering, analogue to penguins (Davenport *et al.* 1984). Others, especially very large species, are reported as barely able to swim, and usually wade on the ground with the body partially out of the water. One such example is the alligator snapping turtle from North America (*Macrochelys temminckii*) (Bonin *et al.* 2006, 114; Mlynarski & Wermuth 1993, 88). What at a first sight seems paradoxical, several tortoises more adapted to a terrestrial life can swim. For example, *Chelonoidis carbonaria, Chelonoidis denticulata,* or *Dipsochelys elephantina* are described as using all limbs to progress in water in a kind of "dog paddle" (Bonin *et al.* 2006, 210, 213, 220).

As we saw above, the evaluation of a taxon concerning swimming ability cannot be based on general statements or common sense, but must take into account the species specific behaviour. Although humans are a well-studied species, for some reasons, the discussion on human ability to swim is characterized by several misconceptions and lack of data. For example, after comparing humans with other mammals concerning their ability to swim, Jan Wind concluded that several human features increase the risk of drowning in this species (Wind 1976; 1991) like limb adaptations associated to human erect posture, the anatomy of larynx, large human brain (which allegedly is more susceptible to lack of oxygen during apnoea). Although these publications have to be acknowledged for addressing a neglected topic, several of Wind's arguments are problematic. For example, to evaluate human swimming and diving performance, it is important to compare humans first with their close relatives, as the most crucial aspect of this performance is related to the loss of instinctive swimming. This however, did not occur first in early or modern hominins, but probably in the last common ancestor of extant hominoids – all hominoids are not able to swim instinctively, so bipedalism and human larynx anatomy cannot be included in this analysis (Bender & Bender 2013). All arguments pointing to human specific features therefore are misleading. Compared with other extant hominoids, humans are certainly "good" swimmers and divers, as they interact with water in a way which regularly leads to swimming and diving ability (see chapter 5.5).

Wind's arguments that drowning is common in humans is based on facts: according to the World Health Organization, in 2012 drowning was the 3rd leading cause of unintentional

injury death worldwide, accounting for 7% of all injury related deaths (WHO 2012). However, it is a fallacy to conclude that "the human proneness to drowning [...] shows that the capacity to survive in the water must have gradually decreased during human phylogeny" (Wind 1991). By using arguments connected to human bipedalism and large brain, Wind implies that this alleged gradual decrease of capacity to survive in water occurred after the chimpanzee/human split. The lack of logic is related to the assumption that a species A with a higher mortality than species B concerning a certain cause of death can be interpreted as a proof that species A is "less adapted" than species B concerning the interaction with aspects of the environment linked to this cause of death. For example, beavers are sometimes killed by falling trees (Kile & Rosell 1996), while whales most probably are not; this does not mean that whales are "better adapted" to fell trees than beavers. Gibbons often fall from trees and fracture their bones. Schultz found in a "series of 260 skeletons of wild adult gibbons thirty-three per cent with at least one healed fracture" (Schultz 1969, 194). He continued: "For wild orang-utans the corresponding percentage amounts to thirty-four, but among the far less arboreal African great apes fractures exist not nearly as often, though no more rarely than in many monkeys" (Schultz 1969, 194-195). Similarly, the fact that non-human hominoids probably drown less frequently than humans cannot be interpreted as an indication that non-human hominoids are better swimmers than humans, since humans undoubtedly interact far more often with water than non-human hominoids (see chapter 5). To sum up, arguments addressing swimming ability in humans have to consider primary anatomical, physiological and behavioural traits in this last common ancestor which first lost the ability to swim instinctively, not in humans. For the same reason, human ability to swim and to dive has to be compared with the swimming and diving ability (or lack thereof) in the close relatives (extant hominoids) or in other vertebrates which lost the ability to swim instinctively.

3.6 Guidelines for the convergence approach

The convergence approach is conceived as an attempt to standardize the use of convergences as a tool and as an additional aid in functional analyses. The here proposed approach can be used as a starting point for future developments of a formalized method expressed in an algorithm format. Such a method has to acknowledge problems of comparing organisms from distantly related taxa with very different body plans, such as insects and mammals, and entails problems related to scaling relationships. Instead of such a formalized and general method, theoretical aspects of functional analyses and operational rules for assessing adaptation using comparisons between hominins and other vertebrates are here discussed; a similar approach was expressed by other authors (Kay & Covert 1984).

The following guidelines summarize and complement the most relevant aspects of the convergence approach discussed in the present chapter.

(1) Use convergences as a tool in functional analyses whenever possible, or explain why you do not use convergence; for example, in cases in which a uniqueness of traits is assumed.

Explanation: The use of convergences is one among several approaches in functional analyses. Convergences help us to understand which traits are likely to have an adaptive function associated with a certain environment (see chapter 2.5.1 and Appendix C). Convergences should therefore be used to corroborate hypotheses on the adaptive meaning of traits whenever possible; see also guideline 3.

(2) There are no distantly related species which are “absolutely convergent” – every example of convergence requires the formulation of which traits are convergent and why. The comparison of distantly related species has to be carried out by building well-defined and justified categories.

Explanation: There are several examples of convergences published in the literature (see chapter 2.5) which can provide a first orientation as to how distantly related organisms are functionally related. The method here proposed is based on a stepwise expansion of categories of comparison. As explained above (chapter 3.5), it is important to formulate precisely how the categories are established: at each proposed expansion of the categories it must be defined how the traits of new categories are functionally related. These formulations are essential to determine if the proposed categorization is valid or just a biological constellation (= unreal patterns of similarity, see above). Biological constellations are the product of the unconscious tendency to select information that supports one’s own hypotheses and beliefs (confirmation bias).

(3) In cases where an organism seems to be unique concerning a certain feature, even after the expansion of categories, make your efforts transparent by showing which categories you considered to reach this conclusion.

Explanation: The term “unique” has to be used carefully. For example, bats are the only known mammals able to fly actively; however, in the expanded category “bats as vertebrates” this flying ability is not unique. Humans are among the few terrestrial permanent bipeds with a vertical column. The only exceptions seem to be gibbons and Indriids, which are highly arboreal species rarely moving on the ground, and penguins, which have a strong aquatic

functional focus and have – as part of this focus – their feet placed near the posterior end of the body. Because their specific functional focuses, the bipedalism of gibbons, Indriids and penguins is not comparable with human bipedalism. However, before assuming the uniqueness of human permanent bipedalism, it is important to consider that all extinct hominoids in which anatomical traits point to permanent bipedalism are automatically classified as hominins. This happens inevitably, as permanent bipedalism is the major diagnostic trait in this taxon. As we will see later (chapter 6), this premise has to be questioned, not on the basis of strong empirical evidence, but on a theoretical level.

If a trait, after careful analysis, is still considered as unique, make transparent which categories and expansions of categories you considered to reach this conclusion. This is important, as some alleged unique features can turn out to be not unique at all, but only one variation of a common pattern found in distantly related species. Hypotheses on functionality assuming that a trait is unique can turn out to be highly improbable in the light of real adaptive patterns which developed in connection with real environments (see above, chapter 3.4.3 on Wheeler's sun-streamlined hypothesis, chapter 3.4.2 on some arguments of the aquatic hypotheses, and Appendix D on the historical development of the savannah hypotheses).

(4) Use the term "functional focus" instead of "adaptation" to describe the total pattern of adaptive and non-adaptive features of an organism, especially if you are not sure which were the selective regimes that shaped these traits in the past or if a trait is adaptive or not.

Explanation: The origin of traits and several major steps involved in functional changes of traits are often difficult to be inferred from fossil evidence or from information available from extant relatives. Instead of assuming (as explained above) that (a) Moroccan goats are adapted to climb trees, (b) humans are adapted to swim (or to wade or to dive), or (c) hippopotamuses are adapted to swim in salt water, it is more precise to say that (a1) climbing trees is part of the functional focus of Moroccan goats, (b1) swimming, diving and wading is part of the functional focus of humans, (c1) swimming in salt water is part of the functional focus of hippopotamuses. Because an organism can do something does not mean that this ability was shaped by natural selection (it can be, but it does not have to be).

(5) In functional analyses it is important to consider the ancestral state of the studied trait and to define the theoretical point ("interlocking point") at which this trait fulfils the minimal conditions to perform the hypothesized function.

Explanation: Discussions on interlocking points have several positive effects in functional analyses: they keep us alert concerning the complexity of functional analyses, they are useful to generate new hypotheses, and they force us to give up hypotheses which imply that an ancestral trait evolved for the hypothesized function before reaching the interlocking point; see above the example of the hook (chapter 3.3.2) and the discussion on the origin of flight in birds (chapter 3.3.1) and insects (chapter 3.3.2). Multiple functions of traits and functional changes occur very frequently; discussions on interlocking points have to consider these possibilities.

(6) Collect enough data on the functional focus of the species of interest and of other (also distantly related) species which allow an in-depth analysis of the studied traits.

Explanation: It is important to gather enough data on an organism's functional focus when establishing the comparative groups. This is one of the most time-consuming aspects of the convergence approach (besides historical analyses), as we all tend to rely on information from specialists. However, other specialists do not have necessarily the same perspective intrinsically related to their own research questions. For example, before assuming that chimpanzees are not able to swim due to a small amount of fat tissue (and therefore a high specific gravity) or that humans of a certain region are probably not able to swim because they are exposed to great danger of being killed by aquatic vertebrates, it is important to collect data on swimming ability of chimpanzees and other non-human hominoids (see chapter 4) and on swimming ability in different human populations interacting with large bodies of water in different regions (with and without potential dangerous aquatic predators) (chapter 5). Furthermore, it is necessary to collect data (which is almost absent in the literature) on fat tissue in non-human hominoids and other primates, and test the associations between fat tissue and swimming ability in primates, including humans. An expansion of the categories including data on swimming ability (or lack thereof) in other terrestrial vertebrates will allow a more in-depth analysis of the considered trait. Such an approach using data from species of different taxa will show which traits are likely to be associated to the lack of swimming ability in terrestrial vertebrates. This approach furthermore improves the chance to find promising evidence which might generate new and perhaps stronger hypotheses than the working hypothesis originally proposed.

(7) Hypotheses proposed within the convergence approach must make predictions about new findings which allow their falsification or corroboration, or state clearly when such predictions are not possible.

Explanation: Not all interpretations of non-homologous patterns of similarity have the same explanatory power. Some cases are clear and non-controversial, especially when they involve features found in organisms adapted to extreme environments or bearing traits which can be easily recognizable as part of a specific functional morphology (e.g., flying, digging). However, even what at a first sight seems to be a clear case of convergence, can turn out to be misleading (see chapter 3.3.3 on pseudo-flying fishes). Other cases are less evident and more prone to generate multiple hypotheses and controversial discussions. These examples apply to (a) structures not optimally designed; (b) traits with no easily recognizable function; and (c) traits developed in a specific selective regime and subsequently partially optimized to perform other functions in a new environment. For example, it is difficult to infer from the Bauplan if a terrestrial organism is able to swim or not, as this ability does not require an optimized anatomy (chapter 4.2.6). Hypotheses on the functional meaning of traits should make transparent if the used convergences are controversial or not. This transparency and the precise formulation of categories allow the evaluation of the hypotheses proposed within the convergence approach. All hypotheses should make predictions about which findings would represent a falsification of the proposed models. Hypotheses based on evolutionary events that are not expected to be reconstructable by today's known scientific methods have to be labelled as such; as it will be shown later (see unprofitability hypothesis in chapter 6.6), these hypotheses have to be part of the scientific discussion.

(8) Test your hypotheses empirically or (when not possible) at least with sound thought experiments in order to detect biologically implausible assumptions and oversimplifications.

Explanation: Some hypotheses probably would have never been published if the author had tested the functionality of a trait by simple empirical or thought experiments (see above Ostrom's hypothesis on the evolution of flying in birds, chapter 3.3.1, or the use of air sacs in orangutans to make them "lighter" in the air, chapter 3.4.1). Hypotheses and thought experiments on the adaptive meaning of traits should be critically evaluated by colleagues in order to exclude at least the most obvious confirmation bias in the corroboration of these models, before you invest too much time following a wrong track and certainly before the hypotheses are published. Be sure that the functional analysis works not only in a hypothetical landscape conceived to accommodate implausible ideas on the evolution of traits, but also in real environments.

(9) Instead of uncritically adopting hypotheses on functionality of traits or evolutionary scenarios only because they are compatible with your research program or because they are

accepted by the majority of specialists, invest in historical investigations (or collaborate with historians) to understand how these models emerged.

Explanation: Although it is impossible to be entirely objective towards all aspects pertinent to one's own research, it is important to be aware of possible problems concerning widely accepted hypotheses. Although rarely acknowledged in the literature, a hypothesis can be influential not because it is based on strong arguments or empirical evidence. For example, weak hypotheses can be perceived intuitively as plausible when they were proposed, even if lacking any empirical evidence or when showing several logical flaws. When a research programme is established, our tendency is to discuss aspects within this programme instead of questioning the main premises of the programme. A very time consuming but productive way to detect research programmes based on weak premises is an in-depth historical analysis (see example of the savannah hypotheses in Appendix D and the emergence of evolutionary thought in Appendix B.

CHAPTER FOUR – AQUATIC ACTIVITIES IN PRIMATES WITH SPECIAL FOCUS ON HOMINOIDS

4.1 Introduction

In this chapter data from extensive literature reviews, questionnaire surveys and own observations on water use in primates, with particular focus on hominoids, including humans will be presented. The results will be discussed in a comparative light, including data on water use by terrestrial mammals. Hypotheses on evolutionary implications will be presented here and in chapter 6.

Given the fact that humans are unique with respect to their dependence on culture and technology, water use by humans and nonhuman hominoids (apes) will be treated in separate chapters. Although many humans from different cultures interact with water to a greater degree than that shown by most individuals of extant apes, there is almost no research which focuses on the evolutionary aspect of human water behaviour. As will be shown in the review of this topic (see chapter 5 and references therein), most investigations on human interaction with water have been concerned with specific aspects of human behaviour, such as the research on the historical development of bathing and swimming in different cultures or underwater diving (mostly concerned with diving activities dependent on breathing apparatus). The expression “historical” refers to evidence found by archaeologists or mentioned in ancient literature, but it does not include the phylogenetic meaning of these behaviours.

Other investigations have focused on the improvement of swimmers’ competitive performances, on the prevention of drowning or on the medical aspects of water use, but these works are similar to the historical investigations, in that they are characterised by a lack of evolutionary perspectives. Nearly all ideas taking into account the evolutionary meaning of humans’ interaction with water were expressed by advocates (or critics) of the aquatic hypotheses.

A further point of discussion is that the discourse on water use in humans was mostly based on intuitive data rather than on knowledge gathered from scientific literature. In fact, although humans are undoubtedly the best studied species, there is, as far as can be assessed, no single investigation or systematic review of behavioural patterns related to water use in a representative number of contemporary human cultures. To date we are not able to answer the most fundamental questions on the subject such as: (a) Which patterns of water use are typical

for humans interacting with water in different environmental settings? (b) How frequent are these behaviours? This investigation will be carried out in chapter 5.

A similar lack of knowledge can be found on water use in non-human primates, especially in apes. This topic can be studied in species living in free, semi-free and captive environments. The first statements on apes' reactions to water came from observations on both captive (Cunningham 1921; Falenstein 1876) and wild animals (Forbes 1897; McCann 1933). Buffon wrote on "apes" foraging at the sea shore, reported by Giovanni Francesco Gemelli Careri (1651–1725), an Italian adventurer and traveler:

> Gemelli Careri speaks of one [ape, species?] he saw which cried like a child, walked erect on its hind-feet, and carried a mat under its arm on which it laid down to sleep. These apes (he adds) seem in some respects to be more sagacious than men; for when they no longer find fruits on the mountains, they descend to the sea shore, where they catch and feed on crabs, oysters, and other shell-fish. There is a species of oyster, called taclovo, which weighs several pounds, and often lies upon the shores with its shells somewhat open; but this animal is sufficiently sagacious to suspect they may close upon him, if he uses his paws, first puts a stone between the shells and then he can eat the oyster at his pleasure. (Buffon 1797, vol. 9, 164-165)

An early account on apes as not able to swim was published by Captain Daniel Beeckman in a book entitled *A Voyage to and from the Island Borneo*. In this book he gave an account of his experiences during a visit to southern Borneo in 1712; he wrote that a young captive orangutan "could not swim, but I know not whether he might not be capable of being taught".[34] These and similar reports – aptly revised in 1929 (third printing, Yerkes & Yerkes 1945) – were based on indirect or anecdotal observations of water use in apes.

[34] The full quotation reads as following:

> *The Monkeys, Apes and Baboons are of many different Sorts and Shapes but the most remarkable are those they call Oran-ootans, which in their Language signifies Men of the Woods: These grow up to be six foot high, they walk upright, have longer Arms than Men, tolerable good Faces (handsomer I am sure than some Hottentots that I have seen), large Teeth, no Tails nor Hair, but on those Parts where it grows on human Bodies; they are very nimble footed and mighty strong; they throw great Stones, Sticks and Billets at those Persons that offend them. The Natives do really believe that these were formerly Men, but Metamorphosed into Beasts for their Blasphemy. They told me many strange Stories of them, too tedious to be inserted here. I bought one out of curiosity, for six Spanish Dollars; it lived with me seven Months, but then died of a Flux; he was too young to show me any Pranks, therefore I shall only tell you that he was a great Thief; and loved strong Liquors; for if our Backs were turned, he would be at the Punch-bowl, and very often would open the Brandy Case, take out a Bottle, drink plentifully, and put it very carefully into its place again. He slept lying along in a human Posture with one Hand under his Head. He could not swim, but I know not whether he might not be capable of being taught. If at any time I was angry with him, he would sigh, sob and cry, till he found that I was*

As we will see, most observations of apes interacting with water were gathered from animals kept in zoos, which is the result of a tradition that began in Germany in the early 20th century. In the attempt to simulate nature, Carl Hagenbeck (1909) and the Swiss architect Urs Eggenschwiler developed a zoo in which water moats were used to take the place of bars and fences (Alexander 1983a; Baratay & Hardouin-Fugier 2000). Since apes were known to be reluctant to enter water and unable to swim (and also because of their notorious ability to escape from cages and the high costs and unfavourable aesthetics of cages and fences), water barriers were thenceforward extensively used to constrain these animals in captive and semi-free ranging conditions in zoos worldwide. This has led to several incidents of apes drowning in water moats – often before the perplexed eyes of zoo visitors. More recently, therefore, there has been a worldwide tendency to constrain apes through methods other than water moats, or to design the water moats with the specific purpose of reducing the drowning risk of these species. These attempts generated several publications on the topic (Crandall 1971; Hancocks 1996; Reuther 1976), which are scattered in the specialized literature of the professional zoo and aquarium world.

Another impetus for the investigation of water use in apes came with the publication of the paper *Water-contact behavior of chimpanzees*, by Shannon Angus (1971), in which data on wild and captive chimpanzees was reviewed and a hypothesis on the lack of swimming ability in chimpanzees was proposed (see below, chapter 6.8.1). Later, attempts to review the literature on water use in primates were published by authors interested in early hominin evolution (Ellis 1987; 1991; Kempf 2009; Niemitz 2002; 2010). Although these works genuinely attempted to review data scattered in the literature, there are several gaps of knowledge which still exist in this field. First, most of the data presented in early works or in non-English publications was not considered (as we will see, these data are relevant to an evaluation of apes' interaction with water.) Second, single dubious or misquoted statements on apes allegedly able to swim gathered from popular literature, were not sufficiently verified and therefore mistakenly integrated into some of these reviews. As these erroneous views concern only a few cases, they should not devaluate the above-mentioned reviews. However the concern here is that instead of being eradicated from primatological knowledge, the inaccuracies are being propagated further. Third, by focusing mainly on the presence or absence or of swimming and diving behaviour in primates, these investigations did not

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reconciled to him; and tho' he was but about twelve Months old when he died, yet he was stronger than any Man in the Ship. (Beeckman 1718, 37-38)

identify the broad range of behavioural patterns related to water use that is evident in this group, especially in apes. Finally, human patterns of water use were not investigated in these reviews – a deficiency which prevents an objective comparison between humans and non-human primates concerning aquatic behaviour.

The present study of water use in primates includes four projects. The specific methodology of each project is described at the beginning of the respective sections. The first project (chapter 4.2) is a review on aquatic activities in non-hominoid primates, investigating a variety of different behaviours. As there is so little specialised literature on the subject, the data search strategy had to be adapted in several ways. Data sources included online databases such as ISI Web of Knowledge and Google Scholar, as well as previous literature reviews on the topic, library researches and a questionnaire survey. The results were categorized according to frequently encountered behavioural patterns.

The second project (chapter 4.3) is a comprehensive review of the literature on apes' interaction with water. Similar to the first project, it was based on several sources: online databases, libraries and a questionnaire survey. Again, the results were categorized into commonly found behavioural patterns.

The third project (chapter 4.4) was an observational study, reporting for the first time on swimming and diving behaviour in apes (one chimpanzee and one orangutan kept by private owners in the United States). The results of this project were published in (Bender & Bender 2013).

The aim of the three projects above was to find a representative amount of data to allow for the identification of a broad spectrum of water-related behavioural patterns as observed in a broad range of environmental settings by wild, semi-free ranging and captive primates, with special focus on apes. Parts of this analysis were presented in (Bender *et al.* 2012) and published in (Bender & Bender 2013).

The fourth project (chapter 5) reviewed specific aspects of human interaction with water in a worldwide representative sample of human populations, using data from a specialised database on human cultures and from additional publications. The results were categorized in a similar way to the previous reviews, but additional, human-specific behavioural patterns were added.

All four projects are discussed jointly from the point of view of the convergence approach in chapter 6.

4.1.1 Remarks on the reliability and interpretation of the data

Experimental versus observational data

Knowledge of primates interacting with water in captive, semi-free and free-ranging conditions was rarely gathered by experimental approaches, owing to ethical concerns or to the lack of a specific research programme in this field. Out of necessity, hypotheses on this subject were based on data which was difficult to use in quantitative analyses, the present analysis is no exception. In captive animals, most variables relevant to the development of patterns of water use were not available or difficult to analyse separately. These included, among others, (a) data concerning air and water temperature, and air humidity; (b) physical aspects of captive conditions (e.g., with or without electric fences at the water moats or dimensions of water moats); and (c) behavioural patterns influenced by early captive conditions (e.g., imprinting related to water use in animals raised by humans). On the other hand, captive apes for decades were part of a gigantic unplanned experiment carried out in zoos, sanctuaries, primate centres, private zoos or in places in which private individuals kept apes as pets. Given the high number of animals interacting with water in captivity, the flaws of such non-experimental conditions are compensated by the roughly inferring which behaviours emerge regularly within which specific environmental settings. This data can then be compared with patterns of water use observed in wild animals.

Reliability of data gathered from different sources

A great amount of the data on water use by wild and captive primates is only available from sources which are underrepresented in scientific discussion, such as (a) non-peer-reviewed books, papers and newspapers published in different languages; (b) unpublished reports from zoo keepers, primatologists, or owners of private zoos; (c) videos uploaded on the internet; and (d) statements published on the internet. All information was considered cautiously in the present investigation. This is especially important after finding that – as stated above – single but relevant statements expressed by scientists (especially in popular books or in interviews later published by other scientists) turned out to be of questionable value; unfortunately, some of this information has been included in the scientific literature. For this reason, efforts have been made to confirm all statements published in non-peer reviewed and in scientific publications, when this was possible. It is worth mentioning here that although some zoo personnel asked about drowning of apes kept in their own zoos gave us very detailed answers,

I had the impression that some of these specialists were not eager to communicate on this topic. However, in several cases, the media ensured that these accidents were made widely known, and direct interviews with zoo keepers and other data suggested that the number of drowning-apes in zoos was much higher than commonly assumed.

Given the strong response rate from contacting scientists, one instance was unusual for the complete lack of response after repeated requests to the people (authors, editor, and photographers) who published their documentation of orangutan swimming. Consequently, the evaluation here considered this an indication of misleading or exaggerated information. When confirmation of published material or observations was not possible (because the author is deceased, for example) other criteria had to be used to evaluate the reliability of statements.

One example of a popular book, *The History of Noell's Ark Gorilla Show* by Anna Mae Noell (1979) offered a unique opportunity to evaluate the reliability of data in the true story of a small family-run animal show that toured the eastern seaboard states of the USA between 1940 and 1971. After Anna and her husband Bob retired from traveling in 1971, they established a colony of retired carnival apes at the "Noell's Ark Chimp Farm".[35] According to Peterson and Goodall, this colony was "one of the largest privately owned groups of captive apes in the world, almost thirty altogether" (2000 [first publ. 1993], 209). Since it is now impossible to verify Noell's statements – Bob Noell passed away in 1991, Anna Mae in 2000 – judging the reliability of this work has to be based on other evidence. Certain passages from the book suggest that several of the accounts on apes' behaviours are reliable. For instance, she described several aspects of apes' interaction with water [36] which are at first sight counter-intuitive but compatible with the present review and consistent with observations reported by scientists. Similarly, some of her statements based on memory demonstrate genuine attempts to express real facts.[37] Similar considerations were used to evaluate other works used to extract data for the present review; remaining concerns about reliability of data are expressed in the results section or in the discussion of the data below.

[35] It was there the famous chimpanzee Lucy – kept by Maurice K. Temerlin and his wife Jane Temerlin and later investigated by Roger Fouts – was born (see chapter 4.3.3, passim).

[36] She first described chimpanzees' and gorillas' fear of large bodies of water (Noell 1979, 21, 40, 144); however, in another part of the book she described how a chimpanzee liked to play with water in a tub (Noell 1979, 40); as it will be shown, this behaviour is commonly observed in chimpanzees.

[37] For instance, she expressed her astonishment at seeing a captive wild bird allowed to stay out of its cage; at the same time she was astonished that she could not remember which species of bird she saw (Noell 1979, 202). Similarly, she gave only an approximate age of the chimpanzee 'Joe' instead of implying a precise knowledge of the age of the animal (Noell 1979, 244).

Video footage from YouTube played a significant role in the present work. For instance the first hints about the chimpanzee 'Cooper' and the orangutan 'Suryia' – both showing highly unusual interactions with water – came from videos uploaded on the internet. The scientific importance of such videos is increasing due to the great number of behaviours documented by zoo visitors. According to the zoo director Terry Wolf (Lion Country Safari Zoo, West Palm Beach, USA), zoo visitors are able to capture behaviours on video which remain unknown to zoo staff, and this phenomenon has increased dramatically in recent years with the spontaneous use of mobile phones equipped with video cameras. In most cases, the authors of the YouTube videos were anonymous and no attempts were made to reveal their names in this study. In a few cases, additional information from the video producers was requested.

As aquatic behaviours in apes (and in some non-hominoid primates) are rare, many events had an anecdotal character, i.e., they occurred with single animals or only once. As correctly pointed out by Rollin (2000) and Sarringhaus et al. (2005), describing anecdotal behaviour is valuable for attracting attention to the possibility of rare behaviours, but care has to be taken to describe each incidence accurately, stressing how many animals show the behaviour, if repeatedly shown and under what circumstances. In this way misleading generalizations or exaggerations about rare behaviours can be avoided (Sarringhaus et al. 2005). Pullin and Steward formulated guidelines for systematic reviews on behavioural studies, stressing the need to consider the widest possible range of sources, including published and unpublished data, the internet and expert opinions, in order to avoid publication bias (Pullin & Stewart 2006). These guidelines have been followed here; the same approach was also followed by the previous reviews on the topic.

4.1.2 Ethical considerations on the use of data of privately kept apes

Noell's book *The History of Noell's Ark Gorilla Show* is also useful to introduce the current section on ethical issues related to the scientific use of data of privately kept apes – this topic is especially relevant after Stephen Ross expressed criticism concerning this topic (see below).

The precarious conditions in which the animals were kept by Noell, as well as their use of chimpanzees for the show – the animals had to wrestle challengers from the public – is equally ethically indefensible. Additionally, the holding conditions of the colony were hazardous, and after criticism expressed by animal rights activists throughout the 1990s, the owners of the colony were forced to close their doors to the public when the U.S. Department

of Agriculture revoked its federal exhibition license in 1999.[38] Although I am *very* sceptical about keeping apes as pets or using these animals in TV, film and ads,[39] it is argued here that the use of data from this and similar books is ethically acceptable, as long as it is used not to motivate other people to keep apes privately, but only to close gaps in scientific research and improve the conditions of apes kept in other artificial environmental settings. I defend the same view concerning the observational studies carried out on the chimpanzee 'Cooper' and the orangutan 'Suryia' – both showing highly unusual interactions with water and both kept privately. Recently Ross (2013) raised ethical concerns regarding the use of privately owned apes in anthropological research, referring specifically to our recently published article where swimming and diving behaviour of 'Cooper 'and 'Suryia' was supplied (Bender & Bender 2013). In a reply to Ross we wrote:

> We agree with Ross that the welfare of animals should always be central in any research project involving experiments on, or observations of animals, including apes. However, we do not accept Ross' implication that gathering and publishing data on privately owned apes is a legitimation of these holding conditions. As well known, apes are prone to drowning in zoos, since water moats are used to constrain these animals. These accidents occur among others because apes are rarely habituated to deep water in captivity. One of the goals of our work on primates' interaction with water is to understand how water can be used in a safe manner to enrich the environment of captive apes. Our research on privately owned apes is only a small part of the project, which includes data on behavior observed in animals living in different environmental settings (e.g., wild and feral animals, animals kept in sanctuaries, research centers, semifree ranging conditions, and public zoos). Although we agree that private individuals should not own primates, we argue that the ethical discussion regarding holding conditions of captive apes should not be limited to privately owned apes, but include all types of captive settings. We would also like to clarify that we have ethical clearance from the Animal Ethics Screening Committee of the Witwatersrand University for our study. (Bender & Bender 2014, 165)

Similar ideas were expressed by Marc Bekoff, Professor Emeritus of Ecology and Evolutionary Biology at the University of Colorado, Boulder, in *Psychology Today.* After he

[38] See http://www.floridamemory.com/audio/podcast-single.php?id=23, and http://www.tampabay.com/news/environment/wildlife/suncoast-primate-sanctuary-reopens-to-the-public/814279, both accessed on 1st January 2014). The colony has received a new license and reopens to the public in 2008 under the name Suncoast Primate Sanctuary; see Rita Farlow in http://www.tampabay.com/news/environment/wildlife/suncoast-primate-sanctuary-reopens-to-the-public/814279, accessed on 14 January 2014.

[39] See a book written by a veteran of People for the Ethical Treatment of Animals (PETA) (Guillermo 1993).

published an article entitled *Apes Swim and Birds Know Speed Limits*[40], the article, as Bekoff stated, "prompted a few people to note that the observations of the orangutan swimming were made at a non-accredited facility."[41] Bekoff asked if we should use data from such facilities for scientific purposes, and continued: "People disagree and I feel this question will be of interest to readers of Psychology Today. My own take is that it is acceptable to use these sorts of existing data with some very strong restrictions especially for future research. And, the data must be used for the animals' benefit".[42] This statement basically reflects my opinion on the subject.

As stated above, ethical discussion regarding holding conditions of captive apes should not be limited to privately owned apes, but include also animals kept in accredited facilities. An important point in the discussion on apes in public zoos concerns the conflict of interests between welfare of animals and the expectations of paying visitors – this conflict is fundamental in the criteria used to design the zoos. I wrote on this topic in a reply to Bekoff's paper mentioned above:

> An important aspect of exposing apes in a public zoo is the conflict of interests between welfare of apes on the one hand and the expectations of paying visitors on the other hand, which is fundamental in the criteria used to design the zoos. One of the most insightful examples of this conflict is related to the way how apes in public zoos are constrained. Many public zoos use deep water moats for this purpose, a solution that was believed to be safe (at least for the public) and aesthetically superior to fences (again, from the point of view of most zoo's visitors). However, several accidents with apes drowned in water moats showed that this concept is problematic. For this reason, there is a tendency in modern zoos to design new enclosures without the use of deep water moats, a fact that is well known by specialists. [43]

As a result of this development, zoos are being designed to exclude apes' contact with large water bodies almost completely, without taking into consideration knowledge from alternative concepts in which apes can be habituated to water in a safe way. However, there are alternatives to these sweeping measures:

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[40] In http://www.psychologytoday.com/blog/animal-emotions/201308/apes-swim-and-birds-know-speed-limits, accessed on 14 January 2014.
[41] In http://www.psychologytoday.com/blog/animal-emotions/201309/research-data-should-we-ignore-studies-abused-animals, accessed 14 January 2014).
[42] In http://www.psychologytoday.com/blog/animal-emotions/201309/research-data-should-we-ignore-studies-abused-animals, accessed 14 January 2014).
[43] Renato Bender, in http://www.psychologytoday.com/blog/animal-emotions/201309/research-data-should-we-ignore-studies-abused-animals/comments, submitted on 3 October 2013; accessed on 14 January 2014.

> For instance, the Arnhem Zoo in the Netherlands developed a method to facilitate habituation to water of chimpanzees with no previous experiences with deep-water moats (van Hooff 1973). In the Lion Safari Country Zoo in West Palm Beach, after drowning cases occurred in the context of intraspecific conflicts, single chimpanzees were consequently isolated as soon as serious social conflicts were observed, and later reintegrated in the group. This preventive measure reduced the accidents in water (interview with Terry Wolf); see also the concepts concerning the use of water as enrichment described by (Brown et al. 1982; Golding 1972). The examples of the apes described in our paper and other apes living in sanctuaries or private and public zoos [reviewed here] demonstrate the degree of safe habituation that can be reached in apes. [44]

As pointed out below, we argue that the guidelines for the design of ape exhibitions in public zoos can be improved by the present review:

> These guidelines (Ross & McNary 2009), although certainly formulated as a genuine attempt to improve the conditions of captive apes, are insufficient to advise zoos and sanctuaries competently concerning the specific topic "apes' water contact". This is a central aspect of this issue: although we definitively do not agree that apes should be kept by privates, the experience of some apes kept under private conditions proved to be useful to improve our knowledge on how apes can be safely habituated to water and how water can be used as environmental enrichment.[45]

Although the use of water as enrichment for captive apes is not the focus of the present work, some basic aspects of this discussion will be discussed below (chapter 4.3.6).

4.1.3 Definitions of the terms "water use" and "swimming"

Water use: refers to behaviours related to an organism's interaction with water. In a strict sense, this term applies to behaviours displayed by an organism when it is inside of water, such as during swimming, diving partially or completely, wading and drowning. In a broader sense, this term also includes behaviours in which an organism does not enter a body of water, such as during drinking, exposure to rain, while crossing a river using natural bridges or playing with water (e.g., water from a hose or water in a tub, with the animal standing outside the tub).

[44] Renato Bender, in http://www.psychologytoday.com/blog/animal-emotions/201309/research-data-should-we-ignore-studies-abused-animals/comments, submitted on 3 October 2013; accessed on 14 January 2014.
[45] Renato Bender, in http://www.psychologytoday.com/blog/animal-emotions/201309/research-data-should-we-ignore-studies-abused-animals/comments, submitted on 3 October 2013; accessed on 14 January 2014.

Swimming: refers to progress in water by self-propulsive, spatially oriented movements. Consequently, the following behaviours are *not* considered as swimming:

(a) Passive floating: The word "swimming" in popular use is defined in several languages to mean "to float in water or another liquid" as well as to mean active swimming as defined above, although it is generally possible to recognize from the context if the term applies to a passively floating or to self-propulsive swimming organism. Surprisingly often there are intentional or unintentional misinterpretations of the term, for instance in connection to "baby swimming"; see Bender (1999, 84-85) where it is shown that human babies are not able to swim according to objective definitions of swimming). (b) Movements in water that are not part of spatially oriented and clearly propulsive movements, but are commonly called "swimming" (for example in the alleged "baby swimming"). (c) The uncoordinated movements of an organism during an apparent desperate attempt to escape water (e.g., observed when an ape or a human unable to swim falls accidentally into water). Although this may coincidentally result in progressing a short distance in water, it was not considered as swimming for the purpose of this study (see chapter 4.3.4 on orangutan). (d) Progress in water by pulling or pushing something other than the water (see chapter 3.2.1 on hippopotamus in fresh-water, chapter 4.3.5 on chimpanzee observed crossing a moat under water, and chapter 4.3.4 on what seem to be orangutans wading or holding onto branches).

4.2 Aquatic activities in non-hominoid primates

4.2.1 Introduction

Data on water use is still unknown for many primate species. There are only a few reviews on this topic (Ellis 1986; 1987; 1991; Kempf 2009; Niemitz 2002; 2010). These investigations suggest that several non-hominoid primate species are known to be regular or occasional swimmers. Ellis (1991) reported that at least six species of primates have been recorded as swimming when free-ranging and another 12 have been recorded swimming or wading in zoos. Niemitz added five more primates species to this compilation (Niemitz 2002).[46] In her review of water use in primates, Kempf wrote that at least 30 primate species have been reported to interact with aquatic environments, pointing out that "the reasons for these interactions and their general significance in primate ecology and adaptation are not well understood" (Kempf 2009, 275).

[46] The same author listed 49 species of Old World monkey and ape species in an attempt to specify their ecological or behavioural relationship to a shore or body of water in the wild (except for dependence on drinking water) (Niemitz 2010); see below on the problems related to inferring directly from ecological data to behavioural traits concerning water use.

Factually, vast areas concerning water use in primates are *terra incognita*. In the following review I will try to close some gaps on the subject, presenting data from different sources and considering different aspects of non-hominoid primates' interaction with water.

4.2.2 Methods

As there is little specialised literature on the subject, the data search strategy had to be adapted in several ways. Data sources included (a) the online databases ISI Web of Knowledge and Google Scholar using a broad search strategy such as "primates AND water" as well as specific search terms, such as "swimming", "diving", "wading" and "drowning", all combined with the term "primates"; (b) previous literature reviews on the topic; (c) books and book chapters from my own library (over 540 books, book chapters and papers on primates) and from the libraries of the Universities of Bern and Basel in Switzerland, as well as from the University of the Witwatersrand; (d) further data on primates' interaction with water was gathered through a questionnaire survey carried out among chosen zoos, sanctuaries and primatologists, for species or genera where information on water use was missing in the literature.

To improve the response rate[47], the questionnaire asked a few, simple and open-ended questions on observations of primates' interaction with water, including playing in or at water, wading, feeding in water, sitting in water, swimming, submerging and drowning. The questions were as follows: (1) Do you know of any published or unpublished report on swimming in [*species or family*] in the wild or in captivity? If yes, can you give more details about these reports? Please specify the species, if possible. (2) Are there [*family*] species known by direct observation or indirect evidence not to be able to swim? We are also interested in reports on [*species / families*] with poor swimming ability (e.g., species known to swim only a couple of meters). (3) Are there [*family*] species able to swim, but reluctant to enter water? We classify a species as reluctant to enter water like in cases where a group does not try to escape from an island surrounded by a narrow water moat. (4) Do you know of any other behavioural patterns towards water like diving, drowning, use of water for thermoregulatory purposes, wading, feeding in or at water, playing in water, in [*species /*

[47] A list of all zoos, sanctuaries and primatologists contacted is not available, as this research began in the early 1990s as a side project aiming to add information to the extensive literature review. As a result, no record was kept of the persons contacted; only their answers were collected. Therefore, the exact response rate can not be given. Additional answers about non-hominoid primates were also received from primatologists and other specialists working with apes, so that there is no clear delineation between this survey and the one carried out for the apes.

family]? (5) Are there further specialists that you think I should contact in this regard? (6) Do you know of any publication on this topic that could help me further?

The behaviours recorded include swimming, diving, wading, foraging in / at water, playing in water, bathing/thermoregulation in water, escaping from predators in water or being preyed on in water and washing food or other objects in water. Data on riverine or swampy habitats were not considered, as it does not inform on specific water use in primates. For delimitation, data on drinking water in non-hominoid primates were not especially considered; data concerning drinking behaviour gathered unsystematically is not presented here (unpublished material).

Only data on non-hominoid primates are considered in this review. First overall results are given in a quantitative overview. Afterwards, selected results are reported in more detail to better reflect the patterns of water use found in this review. These reports are divided into two groups of water use: swimming and diving (and reasons for these behaviours) on the one hand, and behaviours related to foraging in/at water on the other hand. When it was not possible to divide the two behaviours, in single cases both behavioural aspects were reported together. In some cases a genus was given in the literature instead of a species to describe a specific behaviour. For this reason results are given at the level of species and genus.

4.2.3 Overall results

According to the literature consulted and the answers from the questionnaire survey, the overall numbers of species and genera showing the behaviours assessed are as follows:

- 39 species (from 20 genera) were reported able to swim
- 24 species (from 14 genera) were reported feeding in or at the water
- 14 species (from 8 genera) were reported wading
- 9 species (from 4 genera) were reported diving and swimming under water
- 8 species (from 4 genera) were reported playing in water
- 8 species (from 6 genera) were reported escaping into water from terrestrial predators or conspecifics
- 6 species (from 2 genera) were reported bathing and/or seeking thermoregulation in water
- 6 species (from 3 genera) were reported washing food or other objects in water
- 3 species (from 2 genera) were victims of aquatic predators like crocodiles

When only a whole genus for a specific behaviour was named, it was counted as one species. The numbers given here are therefore very conservative. See Table 4.1 for the results by genus and species, with references. For more detailed descriptions of chosen behaviours (including an overview of swimming in terrestrial mammals) see below (chapters 4.2.4, 4.2.5 and 4.2.6). The complete results can be requested from the author.

Table 4.1 Selected references for aquatic activities in non-hominoid primates

Genus / species	Swimming	Diving	Wading	Feeding	Playing	Bathing / Thermo	Predators	Washing
Genus *Hapalemur* (*Hapalemur griseus*)	Dog paddle (Kavanagh 1983, 42-43; Petter & Peyrieras 1975, 283).			Papyrus (Mutschler et al. 1998); bamboo (Kavanagh 1983, 43).				
Genus *Loris* *(Loris lydekkerianus)*	Not able to swim (Bishop 1963; Pocock 1939)							
Genuis *Galago* (*Galago senegalensis*)	Poor swimmer (Kenmuir 1982, 27; Lagus 1960, 163)							
Genus *Carlito* (*Carlito syrichta*)				Shrimps and fish in captivity (Niemitz 1979)				
Genus *Tarsius*				Shrimps and fish in the wild (Berger 1984, 59)				
Genus *Callithrix*	Not able to swim, drown (van Roosmalen et al. 2002, 41); all callitrichidae swim with ease (Hershkovitz 1977, 448); dog-fashion (Hershkovitz 1977, 560)							
Genus *Saguinus* (*Saguinus geoffroyi*)	Good swimmer, dog-fashion (Hershkovitz 1977, 798)							
Genus *Cebus*	(Schultz 1969, 45); Bender and Bender, own observation			Oysters at sea shore (Kavanagh 1983, 98).				
Cebus olivaceus								Food in zoo (Urbani 2001)

Genus / species	Swimming	Diving	Wading	Feeding	Playing	Bathing / Thermo	Predators	Washing
Genus *Sapajus* (*Sapajus apella*)				Crustaceans (Port-Carvalho et al. 2004) ; using a tool to open oysters (Fernandes 1991); ostrea and frogs (Freese & Oppenheimer 1981); fish (fishing with a bait) (Mendes *et al.* 2000)				Objects and food in lab (Visalberghi & Fragaszy 1990a)
Genus *Saimiri*	Marc van Roosmalen, pers. comm.							
Saimiri sciureus				Frogs and crabs (Baldwin & Baldwin 1981)				
Genus *Callicebus*	Not able to swim, drown, (van Roosmalen *et al.* 2002, 41)							
Genus *Cacajao*	Marc van Roosmalen, pers. comm.							
Cacajao melanocephalus	Dog paddle (Bezerra *et al.* 2011, 55)							

Genus / species	Swimming	Diving	Wading	Feeding	Playing	Bathing / Thermo	Predators	Washing
Genus *Alouatta*	Marc van Roosmalen, pers. comm.; in zoo Constanze Melicharek, pers. comm.; overhand stroke (Carpenter 1934, 33) (but see below references on dog paddle); rare swimmers (Feeley & Terborgh 2005, 122; Milton 1982); anecdotal reports, dog paddle (Collias & Southwick 1952; Feeley & Terborgh 2005)							
Alouatta palliata	(Neville *et al.* 1988, 362); excellent swimmers (Gonzalez-Socoloske & Snarr 2010; Kinzey 1997)							
Alouatta pigra	(Chaves & Stoner 2010)							
Alouatta seniculus	(Feeley & Terborgh 2005, 122; Gonzalez-Socoloske & Snarr 2010; Izawa & Lozano 1990; Kinzey 1997)							
Genus *Ateles*	(Campbell 2000; Milton & Hopkins 2006)		(Crandall 1971, 98)					
Ateles marginatus	In zoo, Tereza C.C. Margarido, pers. comm.							
Ateles Geoffroyi	(Chaves & Stoner 2010)							
Genus *Allenopithecus* (*Allenopithecus nigroviridis*)	(Averill 2000; Maisels et al. 2006; Rowe 1996,147)	(Averill 2000)	In zoo (Novak 1991)	(Averill 2000; fish, Rowe 1996, 147)	In zoo (Averill 2000; Berger 1984, 160)		Escape (Maisels et al. 2006; Rowe 1996, 147)	

Genus / species	Swimming	Diving	Wading	Feeding	Playing	Bathing / Thermo	Predators	Washing
Genus *Miopithecus* (*Miopithecus talapoin*)	(Kanavagh 1983, 184; Napier & Napier 1985, 184)						Sleep over water to escape (Napier & Napier 1985, 184)	
Miopithecus ogouensis				Fresh water shrimps (Novak 1991)				
Genus *Chlorocebus* (*Chlorocebus aethiops*)	(Lagus 1960, 163; Robins & Legge 1959, 62)			Fiddler crabs (Fedigan & Fedigan 1988)				
Genus *Cercopithecus*	(Schultz 1969, 45)							
Cercopithecus mitis	(Gautier-Hion & Gautier 1976)							
Cercopithecus mona	Pers. comm. of R. Kagan, Dallas Zoo, to Ellis (1987, 366); in the wild: Sanderson (in Berger 1984, 139)							
Cercopithecus neglectus	pers. comm. of D. Bourne, Toronto Zoo, to Ellis (1987, 366)			Invertebrates from river bank (Wahome et al. 1993)				
Cercopithecus cephus	(Rowe 1996)						Escape (Rowe 1996)	
Genus *Macaca* (*Macaca sylvanus*)	In zoo, Constanze Melicharek, Apenheul Primate Park, pers. comm; pers. comm. of R.W. Shumaker, National Zoological Park, to Ellis (1987, 366)			Tadpoles and amphibians (Mehlman 1988; Rowe 1996, 133).		(Kempf 2009)		

Genus / species	Swimming	Diving	Wading	Feeding	Playing	Bathing / Thermo	Predators	Washing
Macaca silenus	(Fooden 1986; Roonwal & Mohnot 1977)			(Robins & Waitt 2011)		(Freeman 1977, 69; Napier & Napier 1979, 96)		(Napier & Napier 1979, 96)
Macaca nemestrina	(Fooden 1986; Roonwal & Mohnot 1977)		(Niemitz 2002)	(Niemitz 2002); river crabs: (Rowe 1996, 128).				
Macaca nigra	Pers. comm. of R.W. Shumaker, National Zoological Park, to Ellis (Ellis 1987, 366)		In zoo (Blount 1998); Bipedal: (Niemitz 2010).	In zoo (Blount 1998)				
Macaca fascicularis	Good swimmers, (Wheatley 1980, 221); Polly Schultz, Wisconsin Primate Research Center, in: (Kirby *et al.* 2006); (Fittinghoff & Lindburg 1980, 205-206; Fooden 1986; Roonwal & Mohnot 1977; Rowe 1996, 123; Van Schaik et al. 1996). In zoo, (Du Mond et al. 2000).	In zoo, Jill Rawlins Oregon Primate Research Center, and Polly Schultz, Wisconsin Primate Research Center, in: (Kirby *et al.* 2006); (Anderson et al. 1992; Anderson et al. 1994; Du Mond et al. 2000; Fittinghoff & Lindburg 1980, 206).	Bipedal: (Niemitz 2010).	(Schultz 1969, 45); fish (Stewart *et al.* 2008). Crabs, (Son 2003; Sussman & Tattersal 1986); Stone tools to access prey (Gumert et al. 2009; Malaivijitnond et al. 2007; Wheatley 1988); Oyster (Gumert & Malaivijitnond 2012; Rowe 1996, 123).	(Anderson *et al.* 1992)	(Van Schaik *et al.* 1996)	Escape (Van Schaik *et al.* 1996)	Food (Wheatley 1980, 223; Wheatley 1988). In lab all sorts of objects (Visalberghi & Fragaszy 1990a).
Macaca acroides	Swim well, enjoy water, (Fooden 1986; Stonor 1944).			Water snails in shallows (Estrada & Estrada 1977).				

Genus / species	Swimming	Diving	Wading	Feeding	Playing	Bathing / Thermo	Predators	Washing
Macaca mulatta	Dog paddle (Berman 1977, 761; Fooden 1986; Fooden 2000; McGraw 1939; Muir 1916; Roonwal & Mohnot 1977; Sterndale & Finn 1929, 17). In captivity (Anderson et al. 1992; Dunbar 1989; Ellis 1987, 366; Rawlins 2005, 1-2; Riopelle & Hubbard 1982).	(Muir 1916; Sterndale & Finn 1929, 17); in captivity (Robins & Waitt 2011); Natasha Down, York University, in (Kirby *et al.* 2006); (Anderson et al. 1992; Rawlins 2005, 1-2; Riopelle & Hubbard 1982).		(Fooden 2000); in captivity (Rawlins 2005, 1-2).	(Berman 1977, 761; Fooden 2000); in captivity (Anderson et al. 1992; Rawlins 2005, 1-2).	(Anderson et al. 1992; Fooden 2000; Kawai 1965; Zhang et al. 2007).	Escape (Fooden 2000; Muir 1916).	Food (Fragaszy & Visalberghi 1996; Robins & Waitt 2011).
Macaca fuscata	(Fooden 1986; Gonzalez-Socoloske & Snarr 2010; Hirata et al. 2001, 497-499; Kawai 1965; Kawai 1975; Roonwal & Mohnot 1977; Rowe 1996, 124).	(Kawai 1965); in zoo, Bev Carter, pers. comm.; (Hirata *et al.* 2001, 497-499).	In zoo, Bev Carter, pers. comm. (Hirata *et al.* 2001, 497-499); bipedal (Niemitz 2010).	Shells and shrimps (Kawai 1975; Schultz 1969, 45); fish and octopi (De Waal 2001) ; (Leca et al. 2007; Watanabe 1989; Zhang et al. 2007) ; in zoo: Bev Carter, pers. comm.; (Nakamichi et al. 1998; Rowe 1996, 124; Suzuki et al. 1990).	(Hirata et al. 2001, 497-499; Zhang et al. 2007).	(Hirata et al. 2001, 497-499; Hori et al. 1977; Kawai 1975; Zhang et al. 2007).		grass roots (Nakamichi *et al.* 1998); sweet potatoes in sea water (Hirata *et al.* 2001, 494); (Rowe 1996, 124).
Macaca sinica	(Fooden 1986; Roonwal & Mohnot 1977) ; Frog-style (Steward 1886).	(Niemitz 2010; Steward 1886).	Bipedally (Niemitz 2010).	(Niemitz 2010).			(Kempf 2009).	
Macaca radiata	Dog paddle (Agoramoorthy *et al.* 2000; Fooden 1986; Roonwal & Mohnot 1977; Simonds 1965, 189).	(Agoramoorthy *et al.* 2000).			(Simonds 1965, 189).			
Macaca thibetana	(Fooden 1986; Roonwal & Mohnot 1977).							

Genus / species	Swimming	Diving	Wading	Feeding	Playing	Bathing / Thermo	Predators	Washing
Genus *Papio*			Quadrupedally (Napier & Napier 1979, 81).				Reluctant to enter water, possibly because of crocodiles (Napier & Napier 1979, 81).	
Papio hamadryas	Jimmy Magill, Gerard de Nijs, Debby Cox of Jane Goodall Institute, in (Eckert *et al.* 1999); Avoid water (Berger 1984, 134).				Sylvia Corte, Universidade de la República, Uruguay, in (Eckert *et al.* 1999).			
Papio anubis	Gerard de Nijs in (Eckert *et al.* 1999); (Goodall 1990, 29; Lawick-Goodall 1971, 45).	(Forthman 1999; Pfeyffers 1999).	(Goodall 1990, 29; Lawick-Goodall 1971, 45).	Fish and crabs (Goodall 1990, 29; Lawick-Goodall 1971, 45; Stewart et al. 2008).	(Forthman 1999).		Escape from aggressive conspecifics (Goodall 1990, 29).	
Papio cynocephalus	Bearder, pers. comm. to (Niemitz 2002).		Bidedal (Niemitz 2010).	Crabs (Messeri 1978; Nishida 1980).			Crocodiles, have specific alarm call (Fischer *et al.* 2001).	
Papio ursinus	(Hall 1963); also indirect evidence for drowning (Hall 1961); (Anderson et al. 1994; Cheney et al. 2004; Child 1968, 47; Lagus 1960, 163).	(Robins & Legge 1959, 63; Wrangham 2005).	(Hall 1963).	Shellfish, black mussels (Hall 1963; 1961); Matthew Lewis, pers. comm.; fishing in waterholes (Hamilton III & Tilson 1985); fish (Stewart *et al.* 2008); aquatic plants (Hamilton III et al. 1976); roots of aquatic plants (Child 1968, 48).			Crocodile (Cheney *et al.* 2004; Enstam 2007).	

Genus / species	Swimming	Diving	Wading	Feeding	Playing	Bathing / Thermo	Predators	Washing
Genus *Theropithecus* *Theropithecus gelada*	(Aguiar in Eckert et al. 1999; Schultz 1969, 45)							
Genus *Cercocebus*	(Schultz 1969, 45)							
Genus *Mandrillus* *Mandrillus sphinx*	D. Bourne, Toronto Zoo, pers. comm. to Ellis (Ellis 1987)			Frogs and crabs (Rowe 1996, 142).				
Genus *Colobus*			(Rogers in Eckert *et al.* 1999)					
Colobus guereza			(Devos et al. 2002; Nishihara 1995; Oates 1978); bipedal (Niemitz 2010).	Water plants (Devos et al. 2002; Nishihara 1995; Oates 1978).				
Genus *Semnopithecus* *Semnopithecus entellus*	(Agoramoorthy *et al.* 2000)		Bipedal and quadrupedal (Nikolei 2003)	(Nikolei 2003)				
Genus *Trachypithecus* *Trachypithecus obscurus*			Rarely, in zoo, R. Kagan, Dallas Zoo, pers. comm. to Ellis (Ellis 1987)		Rarely, in zoo, R. Kagan, Dallas Zoo, pers. comm. to Ellis (Ellis 1987)			

Genus / species	Swimming	Diving	Wading	Feeding	Playing	Bathing / Thermo	Predators	Washing
Genus *Nasalis* *Nasalis larvatus*	(Bennett & Sebastian 1988; Boonratana 2000; Dudgeon 2000; Yeager 1991); dog paddle (Berger 1984, 169; Brandon-Jones 1996; Kawabe & Mano 1972; Kern 1964; Onuma 2002)	(Bennett & Sebastian 1988; Berger 1984, 169; Boonratana 2000; Brandon-Jones 1996; Kawabe & Mano 1972; Yeager 1991)	(Bennett & Sebastian 1988; Boonratana 2000; Kawabe & Mano 1972; Yeager 1991); Bipedal (Niemitz 2010).			(Berger 1984, 169)	Sleeps close to river possibly to defend from predators, (Matsuda et al. 2009); antipredator behaviour against crocodiles, (Berger 1984, 169; Yeager 1991).	

4.2.4 Swimming and diving ability (or lack of such behaviours) in non-hominoid primates

As a rule, statements on primates as unable to swim based on negative evidence or on observation of captive animals not crossing a water moat have always to be considered with caution. For instance, the howler monkeys (genus *Alouatta*) were long considered unable to swim. Recently some data on swimming ability in this species has been published. One incidence of howler monkey swimming in a large river was reported from Honduras (Gonzalez-Socoloske & Snarr 2010). Howler monkeys were observed and filmed while swimming in Lake Gatun in Panama and were described as good swimmers (Katharine Milton, pers. comm.). According to Feeley and Terborgh "howler monkeys are physically capable of swimming, but do so only very rarely" (Feeley & Terborgh 2005, 122). Marc van Roosmalen wrote about swimming ability in primates in South America: "the only monkey genera in the Amazon that know (how) to swim are those that can make a year-round living in seasonally inundated floodplain forest (Igapo as well as Varzea), that is howling monkeys (*Alouatta*), squirrel monkeys (*Saimiri*) and uakaris (*Cacajao*). They can swim and thus are not confined by smaller, less wide rivers" (Mac van Roosmalen, pers. comm.). On the black-headed uakari (*Cacajao melanocephalus*) Bezerra and colleagues reported: "Swimming: Moving in water using their limbs and tail, in a doggy-paddle swimming fashion. We observed swimming 3 times in 2 different groups after the animals accidentally fell into the water of flooded Igapó". Recently data were published on wild spider (*Ateles geoffroyi*) and howler (*Alouatta pigra*) monkeys sporadically crossing a large Mesoamerican river (Chaves & Stoner 2010; on swimming howling monkeys, see also Neville *et al.* 1988). Carpenter reported on howler monkeys escaping from islands by swimming. According to Central American natives, these animals swim "mismo un hombre" (like a man), demonstrating an overhand stroke (Carpenter 1934, 33); however, I am not aware of similar observations published elsewhere on this species; but see chapter 4.2.4 on *Galago senegalensis* making an over-arm stroke.

Little is known about the swimming ability of the owl monkeys (*Atous*), which were – as far as I know – not reported in the literature as have been directly observed swimming. Some indirect evidence comes from the Owl Monkey Project of Argentina. Eduardo Fernandez-Duque (University of Pennsylvania) reported: "Our only experience is of owl monkeys falling in the water. I remember some assistants reporting on this. The monkeys would be fighting/running in the canopy and they fell in the water. I remember someone saying they

saw one running all wet, indicating that it did not drown" (Eduardo Fernandez-Duque, pers. comm.).

Nasalis larvatus is well-known as a regular and good swimmer; it also dives well. Bennett and Sebastian reported on whole groups of *N. larvatus* regularly crossing the Samunsam River in Malaysia (Bennett & Sebastian 1988, 245). These monkeys normally swim at the water surface, but can dive and swim underwater for up to 20 m in case of danger. Another group of *N. larvatus* in Borneo crossed the 20 m wide Menanggul River almost daily (Boonratana 2000, 507). In the same region Boonratana reported also a *N. larvatus* individual crossing the Kinabatangan River, which is up to 150 m wide. Dudgeon noted that the proboscis monkey has webbed fingers and toes and assumed this is to aid swimming (Dudgeon 2000, 243). Brandon-Jones commented on the swimming style: "The proboscis monkey swims well, using a powerful dog paddle, with the head held well above the water" (Brandon-Jones 1996, 329).

A group of monkeys regularly reported as good swimmers are the macaques. Wheatley counted 27 individuals of *Macaca fascicularis* swimming across the Sengata River in Indonesia (Wheatley 1980, 221); video footage on what seems to be wild and captive *M. fascicularis* swimming several meters underwater is available (Anonymous 2007a; Anonymous 2008c; Anonymous 2010a). The stumptail macaque (*Macaca arctoides*) is said to swim well and to apparently enjoy the water (Fooden 1986, 16; Stonor 1944, 591). Rhesus macaque (*Macaca mulatta*) is since long considered as a species showing intensive interactions with water, as in following statement: "At the end of the war a number of immature specimens were placed in the large aviary, previously and now used for parrots, in the London Zoo. This contains a little pond, and the monkeys took to the water with surprising readiness, not only swimming, but diving from the surface and plunging in from a height. The latter, however, they did feet first, and swam with the dog-stroke" (Finn, in Sterndale & Finn 1929, 17). Kawai reported on regular swimming and bathing behaviour of Japanese macaques (*Macaca fuscata*) of the Ohirayama Troop. Not only these macaques warm up in hot springs during winter, but seem also to cool down in water during hot days in summer (Kawai 1975, 38). Agoramoorthy reported on a swimming accident in wild Bonnet macaques (*Macaca radiata*) crossing a salt-water river in Tamil Nadu State in India. The swimming style was described as "dog-like, moving the upper limbs forward" (Agoramoorthy *et al.* 2000, 152). Some individuals swam several seconds under water. Six juveniles did not

dare to enter the water and the dominant male went back to them, led them to a bridge 100 m away and recrossed the river on the bridge with them.

Fooden (2000, 56) summarized published evidence of *M. mulatta* swimming across water bodies up to one km wide. He reported on studies describing this species swimming in search of food, to escape from predators and swimming for pleasure or thermoregulation. To escape from humans and their dogs, a group of *M. rhesus* first climbed trees near a water pool, then let themselves fall into the water and after resubmerging, swam to the far end of the pool (Muir 1916). Another monkey was reported as escaping from predators by swimming is the Allen's swamp monkey (*Allenopithecus nigroviridis*): "The monkeys must therefore swim between the islands and the mainland. They are known for their ability to escape from predators by plunging into water and swimming away" (Maisels *et al.* 2006, 94). A similar strategy is followed by the Angolan talapoin (*Miopithecus talapoin*): "Talapoins are excellent swimmers. They sleep on low branches overhanging the water and thus have an escape route in case of danger" (Napier & Napier 1985, 144).

During the Kariba Dam animal rescue project, observations were made on Grivets (*Chlorocebus aethiops*): "They discovered, for example, that not only are monkeys fine swimmers, but that they are natural 'skin divers' who often go down to great depths and remain submerged for quite long periods, coming up for air only after covering thirty or forty yards under water" (Robins & Legge 1959, 62). Further species reported to regularly swim are baboons, geladas, mangabeys, guenons and capuchin monkeys (Schultz 1969, 45). Constanze Melicharek from the Apenheul Primate Park in Apeldoorn, The Netherlands, wrote: "Other primates, like Barbery macaques, langurs, howler monkeys do swim across ditches, when there are conflicts in the group" (Constanze Melicharek, pers. comm.).

Hall reported that chacma baboons (*Papio ursinus*) of Good Hope Nature Reserve in South Africa have no aversion to immersing themselves in water. He wrote how a group "walked through the shallow water of a vlei [a shallow, minor lake or seasonal pond], some of them drinking and while in the vlei, a severe squabble broke out in which several of the participants were drenched with water. This group and the others that fed off shell-fish, frequently splash through sea-water pools, and confidently sit on rocks at the very edge of the waves" (Hall 1963, 16). In the same report Hall described how a group of about forty baboons was surprised in a large acacia tree where they were feeding as he came around a corner of land in

a motor launch. He continued: “All leapt from the branches into the water, from heights varying up to about thirty feet, the females having infants clasped to their bellies or on their backs. The base of the tree was about ten yards from dry land. The water level came well up to or over their chests” (Hall 1963, 16). On another occasion, in 1961, during the rescue of animals from the Lake Kariba, two baboons (a full-grown male and a young female) were marooned on Mopane trees about 800 meters from dry land. He wrote: “The female, when nearly caught, leapt into the water, and could be seen swimming down through the water at about 45° from horizontal. She was not seen to re-surface. The male was eventually caught, after being shaken off one tree into the water. He swam to an adjacent tree without attempting to dive and swim under water” (Hall 1963, 16). When engaged in getting shell-fish (see section below), the chacma baboons were often very close to the sea, “and would sometimes have to rush away to avoid a wave” (Hall 1961, 561). Occasionally a dead baboon is washed up on shore, “presumably having been caught by a wave while engaged in this activity” (Hall 1961). This is one of the few indirect evidences of drowning in wild primates.

In a private zoo in South Carolina, four young, three year-old olive baboons (*Papio anubis*) were observed diving passively during swimming. When swimming in a dog-paddle style, they sank regularly due to their negative buoyancy and when they hit the bottom “they would bounce up to surface and do it all over again and be able to cross a 40-foot pool” (Baghavan Antle, pers. comm.). Bev Carter, once keeper at the Toronto Zoo, Canada, reported on olive baboons in the Toronto Zoo which “have a waterfall and shallow pool in their outside exhibit which is primarily a play feature. They do spend some time in the water during hot summer days” (Bev Carter, pers. comm.).

Among lemurs, only one species (*Hapalemur griseus*) is reported as able to swim. Petter and Peryrieras wrote: “These vertical supports are usually only 3 or 4 m high, the distances jumped are not large, and the jumps themselves are generally clumsy; one jump provoked by our approach resulted in the individual falling into the water. According to local fishermen, this larger form swims very well, dog-fashion, with the head just protruding from the water; even females bearing infants on their backs can cross canals over 15 m wide" (Petter & Peyrieras 1975, 283). Similarly, Kanavagh reported: “There is a single stock of gentle grey lemurs (*Hapalemur griseus*) inhabiting reed stands in Lake Alaotra, Madagascar, which swim” (Kavanagh 1983, 42-43).

According to van Roosmalen and colleagues, two genera of Platyrrhini (of two different families, Genus *Callithrix* and Genus *Callicebus*) are not able to swim "meaning that an accidental fall into the water will quickly result in drowning" (van Roosmalen *et al.* 2002, 41). Roosmalen wrote that this statement is based on his own observation in the wild and in captivity (van Roosmalen, pers. comm.). Contrary to this statement, Hershkovitz wrote: "All callitrichids swim dog fashion with ease" (Hershkovitz 1977, 448). He reported a specific incident of swimming in *Callithrix jacchus*, quoting Jeremy Mallinson from Jersey Zoo: "In the Jersey Zoo, "a male Common marmoset, *Callithrix jacchus*, jumped off the island into the water in order to escape being caught up, and it swam in a dog-paddle-like fashion a distance of some nine meters (28 ft.) to the shore. If it had not been for the water-logged state of its coat it would have made good its escape up a tree, but the weight of the water handicapped its usual agility"" (Hershkovitz 1977, 560). As both statements are based on single observations it is difficult to make a final judgement on the swimming capability of marmosets.

Pocock wrote on one loris species (*Loris lydekkerianus*): "They are unable to swim, and when put into water merely move their limbs backwards and forwards without making any progress" (Pocock 1939, 179). One galago species (*Galago senegalensis)* observed during the Kariba dam animal rescue project was described as poor swimmer: "The nightape was also a very poor swimmer, with a groping over-arm stroke suggestive of the crawl. The maximum distance these two swam was eight metres" (Kenmuir 1982, 27).

4.2.5 Foraging in/at water in non-hominoid primates

Several non-hominoid primate species are known to explore sporadically or regularly aquatic food resources. Tufted capuchins (*Sapajus apella*) in Eastern Amazonia were observed preying on crustaceans (Port-Carvalho *et al.* 2004), oysters (Fernandes 1991) and fish (Mendes *et al.* 2000). According to Mutschler et al. (1998), the Alaotran gentle lemur *Hapalemur griseus alaotrensis* is living mainly from papyrus and reed in a marshland habitat around Lac Alaotra, Madagaskar. Schultz reported on the extensive consumption of aquatic food by crab-eating macaques (*Macaca fascicularis*) and Japanese macaques (*Macaca fuscata*) (Schultz 1969, 45). Bev Carter, once keeper at the Toronto Zoo, Canada, reported aquatic activities by Japanese macaques once exhibited in this zoo: "During the summer months we filled their moated area (semi-circular at the front of their exhibit) with approximately three feet of water. At a daily scheduled keeper talk food such as grapes, cut up carrots, apples, etc. was thrown into the water, and all animals went into the water in search of

food. Some walked bipedally and picked up fruit from the bottom with their feet, others actually swam under water and picked up what they wanted. Some animals jumped in and others dived in" (Bev Carter, pers. comm.). The subspecies *Macaca fascicularis aurea* in Thailand uses stone tools to open shells. Japanese macaques from the Koshima Troop detached shells from the rocks at the seashore and opened them, using both hands and the teeth (Kawai 1975, 36). Interestingly, the monkeys come to the seashore always at the low tide.

A similar behaviour is shown by chacma baboons (*Papio ursinus*) at the South African coast. K.R.L.Hall investigated these animals between April 1958 and April 1959 in the Cape of Good Hope Nature Reserve and from July to September 1960, both in the Cape and South-West Africa. He observed and filmed baboons eating shell-fish obtained from the coastal rocks for the first time in August and September 1960. He wrote:

> It was seen in two different groups on a total of six occasions. Some of the group would typically run down to the rocks, at low tide on calm days, and forage for shell-fish in the inter-tidal pool or on the seaweed-covered rocks close to the sea. (Hall 1961, 561)

He describes two techniques of feeding:

> Black mussels were pulled off the rocks manually. A break in the shell was then made with the teeth, not, usually, with the large canines but by placing the shell between the back molars. The shell was then prised open with the fingers and the contents eaten. Limpets were usually prised off the rocks with the teeth, the animal bending right down, as in the action of drinking. We did not observe any quick-pouncing action such as might be directed at removing the limpet before it clamped itself to the rock. (Hall 1961, 561)

Hall did not find any evidence of the baboons cracking a mussel shell against a rock. Neither did he find clear evidence of baboons using a stone as a tool to aid in breaking the shell open. (Hall found close to shell fragments a flat triangular-shaped stone, 10 x 15 x 2, 5 cm deep which seemed to be used to hammer the shell. However, he did not observe this behaviour, and mentioned the possibility that these marks might have been done by an angler the previous day.) Matthew Lewis, who is writing a PhD thesis on marine foraging in the same species exploring the same food resources, never did see direct or indirect evidence of a tool used in connection with gathering shell-fish (Matthew Lewis, pers. comm.).

In a further publication, Hall reported more detailed information on chacma baboon foraging for marine food. He reported that "shell-fish eating is a part of the feeding tradition of all the four southernmost groups in the Cape Peninsula, occurring almost daily when wind and tide allow of easy access to intertidal rock-pools and to the sea verge" (Hall 1963, 17). In 1961, he observed that many animals of one of the studied groups (the C group) fed off shell-fish "for periods varying from five to seventy-five minutes on seven separate occasions during a nineteen-day period of observation. On two occasions, the feeding occurred at high water, while, on the other five, it occurred between sixty to zero minutes before low water" (Hall 1963, 17). They consumed black mussels (*Choromytilus meridionalis*) and limpets (*Patella granularis*, syn. *Scutellastra granularis*, and *Patella granatina*, syn. *Symbula granutin*) (Hall 1963, 17). According to Hall, other marine and shore items, such as crabs, sand-hoppers and sea-lice, have been identified from their faeces (Hall 1963, 17). He observed baboons with pieces of sea-weed in their mouths, but he was not able to say whether they were eating this or whether it was attached to a shell-fish (Hall 1961, 652). Hall reported on chacma baboons on the Kariba Island paddling in the shallows in search of food, such as the stems of water lilies (Hall 1963, 16). Messeri reported yellow baboons (*Papio cynocephalus*) feeding on marine food at Sar Unanle, on the southern Somali coast, 20 km South of Chisimaio. During the moist season, a troop of about 20 individuals used to sleep in the Sar Uanle area. During the dry season, baboons lived in the mangrove, six km south, and were never seen to sleep at Sar Uanle. He saw, however, "sometimes in the morning, at low tide, groups of 2-3 baboons visited the Sar Uanle area, wondering [wandering] on the beach. During these visits they were observed feeding on crabs. Remains of *Ocypode cordimanus* and *O. khüli* on the beach and of *O. ceratophthalmus* on the sublittoral platform were then found" (Messeri 1978, 69). He described in some cases crab were captured with a jump, "but in most cases the monkeys sat on their back and dug the holes of the crabs to a depth of 20 cm using both hands" (Messeri 1978, 69). He found a cuttlebone near two excavated holes and mentioned the possibility that it was used as a digging tool.

Tarsius was reported eating shrimps and fish in the wild (Berger 1984, 59) and the Philippine tarsier (*Carlito syrichta*) was reported eating shrimps and fish in captivity (Niemitz 1979). The common squirrel monkey (*Saimiri sciureus*) was observed feeding on frogs and crabs (Baldwin & Baldwin 1981). Allen's swamp monkey (*Allenopithecus nigroviridis*) was reported foraging on the ground and in shallow water (Walker & Murray 1975). Feeding on

shrimps and crabs was also observed in the Gabon talapoin (*Miopithecus ogouensis*) (Novak 1991), the grivet (*Chlorocebus aethiops*) (Fedigan & Fedigan 1988), the de Brazza's monkey (*Cercopithecus neglectus*) (Wahome *et al.* 1993), and the mandrill (*Mandrillus sphinx*) (Rowe 1996).

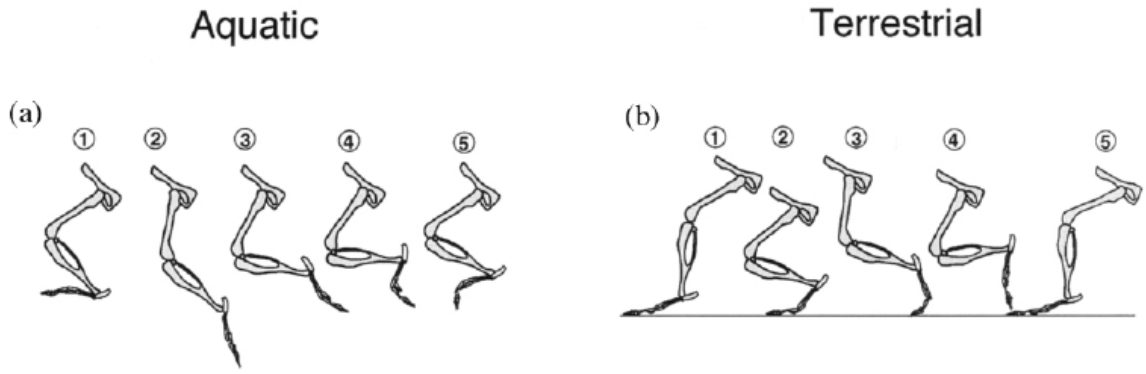
4.2.6 Discussions on water use in primates and other mammals

Swimming in terrestrial mammals

Although swimming is well studied in species adapted to an aquatic environment, this topic is surprisingly understudied concerning mammals lacking obvious aquatic adaptations. Data on this topic is scattered in the literature, and information on swimming ability in several species is often or not existent, or succinct and anecdotal, and sometimes contradictory. Data on swimming mammals used here was gathered from several sources, as for instance from anecdotal observation (Jackson 1961; Krumbiegel 1953) and experimental tests in several species (Dagg & Windsor 1972; Duplantier & Bâ 2001; Hickman 1977; Robins & Waitt 2011; Wilber & Weidenbacher 1961). Several observations on swimming and diving ability in mammals were carried out in connection with wildlife rescues after the formation of artificial lakes; rescues were necessary because several animals were marooned on small temporary islands. We considered here reports gathered in two of these rescue activities: the operation Gwamba, which was carried out to rescue animals trapped behind the Afobake Dam across the Suriname River in Suriname between 1961 and 1964 (Walsh 1967), and the operation Noah, carried out after the damming of the Zambezi River, which led to the formation of the Lake Kariba between 1958 and 1963 (Child 1968; Clements 1959; Kenmuir 1982; Lagus 1960; Robins & Legge 1959). In these operations, both anecdotal and systematic data on behaviour of animals towards water were reported, as for instance distance covered by swimming, relative swimming velocity, degree of reluctance to take to water, tendency to submerge to escape from humans during the rescue activities, etc.

Data from the literature suggests that the ability to swim in terrestrial mammals is widespread. Taking in consideration that swimming behaviour seems to be also widespread in reptiles (see chapters 3.5. and 6.8.2 for reptiles not able to swim or poor swimmers), it is parsimonious to state that instinctive swimming ability is a primitive feature in terrestrial tetrapods. Swimming behaviour is used in different contexts. It is crucial to cross water bodies acting as barriers to dispersal, to expand the home range, search for food and escape from predators (Duplantier &

Bâ 2001; Hickman 1977; Kempf 2009; Wilber & Weidenbacher 1961). Mammals usually swim by transferring their terrestrial gait to an aquatic environment. Most terrestrial mammals progress in water with quadrupedal swimming by moving two diagonal legs simultaneously as in the trot, what is usually called "dog-paddle" (Dagg & Windsor 1972). However, it is certainly wrong to imply that the dog-paddle is an exact reproduction of the terrestrial gait in an aquatic environment. Although little work has been done on how vertebrates use the same musculoskeletal structure to accommodate locomotion in terrestrial and aquatic environment, data are available for some species. For example, analysis of representative species from four vertebrate classes (eels, toads, turtles and rats) demonstrate that "[m]odifications in at least some aspects of the motor program for locomotion appear to be required in order for vertebrates to move effectively through bot aquatic and terrestrial environment" (Gillis & Blob 2001, 72). An example of these modulations of muscle function through which a terrestrial mammal accommodate locomotion in water and on land is shown in Fig. 4.1.



Swimming **Trotting on land**

Figure 4.1 Rat (*Rattus norvegicus*) hindlimb kinematics during swimming and terrestrial locomotion. (a) Schematic representation of the configuration of the skeletal elements of the hindlimbs at several different points (1-5) during swimming cycle. (b) The same representation during a trotting cycle. After Gillis and Blob (2001).

A recent investigation by Frank Fish on swimming in dogs revealed that their swimming movement is closer to the gait on land than to the trot. Fish presented these findings at the Society for Integrative and Comparative Biology (SICB) meeting, held in January 2014 in Austin, TX.[48]

[48] Video footage of this investigation is published in Youtube http://www.youtube.com/watch?v=Xc2wRvR5BHU, retrieved on 10th March 2014.

Strong differences between mammals exist concerning their swimming ability. Some terrestrial species have a pronounced aquatic functional focus, like beavers (genus *Castor*) (Wilsson 1966), otters (subfamily Lutrinae) (Fish 1994), polar bear (*Ursus maritimus*) (Hediger-Zurbuchen & Hediger-Zurbuchen 1964), or star-nosed mole (*Condylura cristata*). Several terrestrial species are adept swimmers, although they are often considered as lacking morphological adaptations to swimming, like several species of cottontail rabbits (*Sylvilagus palustris* and *S. aquaticus*) (Thewissen & Taylor 2007). Other species are barely able to swim a couple of meters (for instance a black rhinoceros, *Diceros bicornis*, after being forced to enter deep water (Child 1968, 52)).

In most species considered as "terrestrial" it can be safely assumed that the features responsible for swimming ability were developed and maintained under specific selective pressure. A large number of terrestrial species swim well enough to cross a water barrier over short or middle distances (see Child 1968; Dagg & Windsor 1972; Jackson 1961; Krumbiegel 1953). Few species, like elephants, are even able to cross large rivers, large lakes, estuaries, or swim several hours from one ocean island to other (Johnson 1980b); see also chapter 3.2.1. For this reason, the term "terrestrial mammals", when implying that these animals do not have specific or recognizable adaptations related to swimming or diving, is misleading. If the distinction between terrestrial and semiaquatic species depends on features specifically evolved in connection with swimming or diving, all terrestrial mammals able to swim are "semiaquatic", and only absolute non-swimmers can be designated as terrestrial. However, this nomenclature would contradict a well-established tradition in zoology.

In the literature, there is no coherent terminology concerning the evaluation of swimming ability in terrestrial mammals, and it is very difficult to predict swimming ability only based on the geographical distribution of species. For instance, it is not advisable to consider a species as "poor swimmer" only on the basis of evidences that gene flow in this species is impeded by large rivers. In fact, rivers act as barriers also to animals able to fly (Hayes & Sewlal 2004). The plains pocket gopher (*Geomys bursarius*) was described as unable to swim (Jackson 1961, 184); however, experiments with *Geomys bursarius* shows that they have considerable swimming ability (Kennerly 1963); other investigators show that *Geomys bursarius*, *G. pinetis*, and *Pappogeomys castanops* are rather good swimmers, at least in calm water (Best & Hart 1976). Rahm (1962) conclude that very small rivers act as dispersal barriers to African brush-tailed porcupines (*Atherurus africanus*), a statement used by

Kortlandt (1974) to describe this species as “poor swimmer”. However, as Rahm reported, experiments in water tanks showed that this species are actually good swimmers (Rahm 1962). Occasionally, the African crested porcupine (*Hystrix cristata*) is described as non-swimmer (e.g., Allison 2007, 147), but according to Robert Johnson, who observed an individual of this species, it swims “fairly well, very much like a dog paddle. All of the quills make her float very well. (In the U.S., porcupine quills are occasionally used as floats for fishing)” (pers. comm.). Another porcupine species (*Hystrix galeata*) is not only able to swim, but was observed to take deliberately to water, perhaps as a behavioural adaptation to ectoparasites (Roedelberger & Groschoff 1963, 136).

It is difficult to infer from the general Bauplan of a species the degree of its swimming ability. Even mammals strongly related to a semiaquatic environment are not necessarily good swimmers in the sense of our definition. For instance, the hippopotamus (*Hippopotamus amphibious*) has a strong aquatic functional focus, but seems to be unable to float and to swim in fresh water – it moves in water by pushing with the feet on the ground (Klingel 1988); see chapter 3.2.1 on the possible swimming ability of this species in salt water. Although black rhinoceros (*Diceros bicornis*) spend several hours daily wallowing in the mud, they seem to be (unlike the Asiatic species) poor swimmers; they avoid deep water, since they seem to have difficulty in holding their heads above the surface (Child 1968, 52). On the opposite, it is tempting to deduce from anteaters’ and bats’ anatomical features (which diverge from the general mammalian Bauplan*)* that these organisms are non-swimmers. However, the Northern tamandua (*Tamandua mexicana*) (Esser et al. 2010) and most species of bats (Jackson 1961; Kolb 1984) are able to swim.

Most mammals are able to keep their heads above water surface when swimming, though most part of the body is immersed. Some animals have difficulty to keep at least nose and mouth above the surface when they have heavy structures placed on the head, like adult male Kudus (*Tragelaphus strepsiceros*) with heavy horns and black rhinoceros (*Diceros bicornis*) (Child 1968). Kudus are considered as strong swimmers, but male kudus get soon tired; swimming male kudus were sporadically observed supporting the weight of their huge horns by resting their heads on the cow’s back in Lake Kariba (Lagus 1960, 162). In the same lake, a waterbuck female was seen carrying her offspring on her back as she made for the shore; the same authors reported that in several occasions animals (species?) were noticed to be “supporting their heads on logs which served as lifebelts” (Clements 1959, 192). Pangolins

are covered with heavy protective scales, which is probably a detriment for these animals to keep a horizontal posture in water. The tree pangolin (*Manis tricuspis*) improves buoyancy during swimming by filling its stomach with air (which is characterized by high mechanical activity (Ofusori & Caxton-Martins 2008)) before entering the water (Pagès 1975). A convergent strategy is used by armadillos (Dasypodidae), which have also to compensate the loss of buoyancy caused by the armor shell and reduction of fur by inflating stomach and intestine with air; alternatively, armadillos can walk on the ground of rivers (Moeller 1988). Krumbiegel mentioned the armadillos of the genus *Cabassous* and *Tolipeutes* as non-swimmers (Krumbiegel 1940, 86; Krumbiegel 1953). However, it would be misleading to consider all animals with high buoyancy in water as "better adapted" to a semi-aquatic life. In a certain sense, the opposite seems to be true: several semiaquatic mammals (like muskrats, beavers, and otters) swim with most part of the body submerged (Fish 1982; 1994; Wilsson 1966).

As mentioned above, swimming ability in terrestrial mammals seems to be very widespread. However, the general statement that all mammals are able to swim sporadically mentioned in the literature (Kolb 1984; Lagus 1960, 90) is certainly wrong. As we saw above, there are no reliable reports on swimming behaviour in several arboreal species in the wild (as for instance apes and several other primate species). It is generally believed that giraffes are not able to swim – at least they were never observed swimming (Crandall 1971).

A classification of animals according to their ability to swim, dive and float is proposed here. This classification is based on physical and neuromotor criteria, and other factors. (a) Some species seem to be able to coordinate swimming movements but have a poor swimming ability when compared to other organisms with similar body size due to anatomical peculiarities (rhinos, some antelopes, perhaps some primates, some chameleons and some tortoises). (b) Some species seem not to be able to swim when suddenly exposed to deep (or even shallow) water, because they lack the ability to coordinate their movements to produce lift. Within this group, some species are able to learn secondarily to swim after a phase of intensive interaction with water (like some hominoids, including humans). (c) Several species show different swimming or diving abilities in different ontogenetic phases (as in humans, hoatzins or penguins). (d) A special case of groups (b) and (c) refers to secondary aquatic animals. Some of these animals need a special phase of interaction with water to be able to

perform species-typical swimming and diving behaviours (as in seals, otters and beavers); for details and references see chapter 4.4.3.

Primates' interaction with water (without hominoids)

The review on non-hominoid primates shows that at least 39 species were reported to swim. These species are distributed over 20 genera. Some primate groups are more frequently reported interacting with water than others. Several macaque species, for example, are regularly reported as swimming, diving, feeding and playing in water, as well as using it for thermoregulatory purposes. Other groups like lemurs or certain platyrrhines are rarely or have never been reported interacting with water.[49] In fact, only one species of lemur (*Hapalemur griseus*) reported to swim was found in the above presented review (see chapter 4.2.4). Only a few primate species are explicitly reported as not able to swim and therefore at risk of drowning when accidentally falling into the water. But as mentioned above, data for some species (*Callithrix*) is contradictory and a final statement cannot be made.

Not all species feel comfortable to the same degree in water, as can be shown in baboons. Hamadryas baboons (*Papio hamadryas*), even if able to swim, seem reluctant to take to water and can be kept on islands surrounded by shallow water moats (Berger 1984, 134). Olive baboons (*Papio anubis*) escape into water from aggressive conspecifics (Goodall 1990, 29), a strategy that can be successful only if the opponent is unlikely to follow into the water. Napier and Napier (1979, 81) describe baboons as reluctant to enter water, possibly because of crocodiles. Yellow baboons (*Papio cynocephalus*) have a specific alarm call for crocodiles (Fischer *et al.* 2001).

Eight species of non-hominoid primates were described as escaping into water from terrestrial predators. However, as we saw, water can also represent a danger – in three species predation by aquatic predators was reported. Sometimes both aspects (killed by aquatic predators/escaping in water from terrestrial predators) were observed in one single species, like in *Nasalis larvatus*. This species minimizes the time spent in water by selection of narrow river crossing locations, by leaping between the crowns of adjacent trees or by jumping from

[49] Peter Kappeler (Department of Anthropology, University of Göttingen) stated on swimming in lemurs: "I can keep my answer short: in >20 years of studying wild lemurs, I have never seen any member of eight species at our study site interacting with water other than in the context of drinking; I also never heard of any other such interactions" (pers. comm.). Similarly, Rainer Dolch wrote: "I am not aware of any swimming behaviour in lemurs at all and have never observed the like" (pers. comm.), an opinion also shared by Erik Patel (Duke University Lemur Center, pers. comm.).

a tree extending over the river into the water, falling as close as possible to the shore (Matsuda *et al.* 2008; Yeager 1991). It is possible that in other species behavioural traits associated to water evolved specifically as anti-predatory strategies. An interesting behaviour concerning captive animals was observed and photographed in 2000 in the zoo Parque Barigui, (near Curitiba, Paraná, Brazil) in a group of *Cebus sp*. (occurrence of hybrids are possible) living on two islands surrounded by deep water. The dominant male was observed hitting the water surface with one hand several times, afterwards standing upright while looking at the water, hitting the water again, standing upright again, and finally jumping into the water and swimming to the other island (probably to mate with other females) (own observation). According to Tereza C. C. Margarido from the *Museu de História Natural Capão da Imbuia, Departamento de Zoológico*, this male was observed swimming between the islands regularly at this time; today, the whole group lives on one single island and no regular swimming behaviour occurs (pers. comm.). It is reasonable to assume that at least some species in zoos interact with water more frequently than in the wild because the fear of aquatic predators is less pronounced, as predation is never experienced or because some species have more contact with water because they spend more time on the ground when compared with wild populations (see chapter 4.3.6 on apes).

Foraging in or at the water seems to be a regularly encountered behaviour in old world monkeys and some platyrrhine genera, like capuchins and squirrel monkeys. Animal food like crabs or shells is collected in aquatic habitats by many primate species; these food items might provide easy-to-collect proteins. To open oysters and other shells, *Macaca fascicularis* was reported to use stone tools (Gumert et al. 2009; Malaivijitnond et al. 2007; Wheatley 1988). This behaviour was compared to coastal foraging in humans (Gumert & Malaivijitnond 2012). A technique remembering the termite fishing by chimpanzees is the shrimp fishing by Japanese macaques (*Macaca fuscata*) of the Shimokita Peninsula (Kawai 1975, 37). The animals hold one arm into the water until the shrimps perch on them. Then the shrimps are collected with the mouth. Drinking behaviour using tools such as leaf sponges or leaf cups was observed in capuchins (*Cebus*), captive squirrel monkeys (*Saimiri*) (Shumaker *et al.* 2011, 85-86) and captive old world monkeys, such as green monkeys (*Chlorocebus sabaeus*), rhesus macaques (*Macaca mulatta*), lion-tailed macaques (*Macaca silenus*) or baboons (*Papio*) (Shumaker *et al.* 2011, 99-100).

Bathing, probably for thermoregulatory and play purposes, was regularly observed in Japanese macaques (*Macaca fuscata*). For the Ohirayama Troop, swimming and bathing on hot days was interpreted as thermoregulatory behaviour (Kawai 1975, 38). Later, also individuals of the Koshima Troop started to bathe in the sea, a fact that led to the interpretation that bathing is a pre-cultural behaviour in this species. Apart from the shrimp fishing, the other aquatic behaviours of Japanese macaques were hypothesized to be a consequence of human influence (Kawai 1975, 47).

4.3 Water use by apes: literature review and questionnaire survey

4.3.1 Methods

Data search was based on several sources: (a) online databases ISI Web of Knowledge and PubMed were used to find peer reviewed publications. The following search terms were used: hominoid, ape, chimpanzee, bonobo, gorilla, orangutan and gibbon, combined with swimming, diving, wading, bathing, crossing river, drowning, water use, and aquatic activity; (b) Google Scholar and Scirus were used to find books, book chapters and theses, using the terms listed above; (c) Google was used to find material such as scientist's website information and discussions carried out in forums on the internet, using the search terms listed above; (d) YouTube was used to find video footage, using the same search terms as listed above (search date: 26.-27.12.2012, 2.390 hits, 720 videos checked); (e) books reporting on hominoid behaviour from the libraries of the Universities of Bern, Basel and the Witwatersrand, as well as publications from my own library were included. In some cases (especially the books from the libraries of Witwatersrand University), only the register and certain chapters in each book were consulted. Interestingly, important data did not only arise from relevant reviews on primates' interaction with water, but were uncovered additionally in different indirect ways.

Further data on apes' interaction with water was gathered through a questionnaire survey carried out among chosen zoos, sanctuaries, primatologists and private owners of apes. To improve the response rate[50], the questionnaire asked a few, simple and open-ended questions

[50] A list of all zoos, sanctuaries and primatologists contacted is not available, as this research began in the early 1990s as a side project aiming to add information to the extensive literature review. As a result, no record was kept of the persons contacted; only their answers were collected. Therefore, the exact response rate cannot be given. Additional answers about apes were also received from primatologists and other specialists working with non-hominoid primates, so that there is no clear delineation between this survey and the one carried out for the non-hominoid primates.

on observations of hominoids' interaction with water, including playing in or at water, wading, feeding in water, sitting in water, swimming, submerging and drowning. The questions changed slightly according to several factors. For instance, when data concerning primates' interaction with water were already available before the contact, questions were formulated taking into consideration this specific information. The questionnaire was sent to institutions or private owners in which previous research showed that certain interesting primates' interaction with water had already been observed, or to places in which previous research suggested animals had free or almost free access to water bodies, as in the case of some zoos, sanctuaries or in the case of private owners of apes in which water was used for enrichment purposes. A total of 98 replies from the questionnaire survey were received. In some cases, the participants were asked to supply further details. Chosen informants in South Africa and in USA were visited and interviewed; in two cases (see third project) own observations were carried out on captive apes.

In the result section, an overview is given first, reporting the number of observations found by behaviour and by species. In the subsequent section, detailed reports of the results are given, again by behaviour and by species, in order to reflect the type of behaviours found in this research. Observations on wild animals are reported first, followed by observations carried out in sanctuaries, in zoos and finally by private owners. As far as possible, details are given of the number of animals involved, number of events and circumstances of the event. The results found in the literature have been given as references. The results of the questionnaire survey were reported as "personal communication", "interview" or "own observation", when appropriate. The behaviours were divided into the following categories (but single behaviours are defined in the respective chapters):

1. Different ways to cross water bodies (jumping, using rocks, fallen trees, underwater bridges or "mobile bridges"), crossing water bodies by using artificial or natural floating items. This excludes swimming and wading
2. Different forms of wading (wading bipedally unsupported, wading bipedally using sticks or similar tools, wading bipedally using floating devices, or wading quadrupedally)
3. Swimming (or unknown forms of locomotion under water) over a distance of 3 m or more

4. Different forms of accidental or intentional “aquatic locomotion” over 0,5 - 2,5 m (excluding swimming according to my definition, chapter 4.1.3)
5. Other forms of accidental or deliberate water contacts (i.e., avoidance of rain, deliberate exposure to rain, head submersion, pouring water on head, allowing to spray water in face, ‘washing’ face, ‘washing’ body, ‘washing’ objects, sitting in water, playing in water, and splash display)
6. Experiments and accidents in water (swimming experiments, drowning, near drowning, rescues by humans, rescues by great apes, possible suicide, using water to drown another individual)
7. Feeding in or at water bodies
8. Drinking behaviours

4.3.2 Overall results

An overview of the reports of aquatic behaviours by species is given in Table 4.2. It should be mentioned in advance that, although aquatic behaviours were described in all apes, the number of reports by behaviour and by species does not reflect the prevalence of the behaviour in the species. The perhaps most important bias concerns the number of observations of specific behaviours per species. For instance, although there are more reports on chimpanzees than on bonobos, this reflects the simple fact that bonobos are less common in wild and captive settings than chimpanzees. However, taking into account this bias, the overview is a reliable tool for the identification of species specific behavioural patterns towards water. For instance, wading bipedally is regularly described in orangutans and in chimpanzees, but while orangutans in half of the reports use sticks to wade in water, this behaviour was (as far as I know) not described in chimpanzees and only once observed in bonobos. Some reports explicitly state the absence of a specific behaviour or are unconfirmed reports from third persons. For instance, “washing the face” of babies is reported for gibbon mothers by a primatologist. However, other primatologists argue convincingly that this observation is highly questionable (and are mentioned as such in the footnotes). These reports are nevertheless considered here, as they are important to demonstrate erroneous interpretations in the past. On the other hand, there is a theoretical possibility that some highly questionable data might turn out to be true (see, e.g., gorillas’ interaction with water, chapter 4.3.6).

Table 4.2 Overview of reports on aquatic activities in apes

	Gibbon		Orang.		Gorilla		Bonobo		Chimp.	
	w	**nw**	**w**	**nw**	**w**	**nw**	**w**	**nw**	**w**	**nw**
1. **Strategies to cross water bodies**										
Crossing water by jumping or using stones				a	b	a		a	b	b
Crossing water with floating item				b						b
2. Forms of wading										
Wading bipedally unsupported		a	a	b	c	a	c	c		c
Wading bipedally with stick			a	b	a			a		
Wading with floating item										a
Quadrupedal wading					a	b	b	b	a	
3. Forms of aquatic locomotion										
Confirmed swimming				a						a
Unconfirmed swimming and other forms of aquatic locomotion										a
Preliminary forms of swimming				a		a				
Involuntary water immersions		a		a						a
Alleged swimming	b*	a		b	a	a			a	b
4. Accidental / voluntary water contact										
Avoidance of rain	a		c	a		a			c	c
Exposition to rain / “rain dance”								a	c	a
Head submersion				b		a		a		b
Pouring water on the head								a		a
Spraying water in the face				a						a
Washing face / body	a	a		b		a				b
Sitting in water				a	a	a	a	c	b	b
Washing food or objects				a		a	b	b	a	b
Playing in water / splash display			a	c	a	b	b	c	c	c
5. Experiments and accidents										
Drowning		a		b		b				c
Lack of swimming in experiments		a								
Near drowning and rescues by humans				a		a				b
Drowning individuals rescued by apes				a		a				a
Possible suicide										a
Use of water to drown other individual				a				a		a
6. Feeding in / at water				b	c		c	a	c	b
7. Drinking	c*		c	a	a	a	a	a	c	b

a: Behaviour observed 1-3 times; b: Behaviour observed 4-15 times; c: Behaviour observed 16 or more times or described as regular behaviour; w: Observations in wild animals; nw: Observations in non-wild animals (living in semi-free ranging or captive conditions); * Includes observations of animals living in unknown environmental settings.

4.3.3 Detailed reports on results by behaviour and by species

1. Different strategies used to cross water bodies (without wading and swimming) / remarks about reluctance to cross water bodies / remarks about apes' awareness of water bodies as a dangerous place

Here different techniques used by apes to cross water bodies are reported. For crossing water bodies by wading or swimming see in the respective sections below.

Jumping, using rocks, fallen trees, underwater bridges or a "mobile bridge-technique" / reactions towards electric wires at moats

Orangutans (*Pongo pygmaeus*)

In a documentary[51] three different orangutans (probably from a rehabilitation centre) are shown trying to cross a small river. One adult female with an infant on her shoulders tried to cross the river holding a small trunk but without success. Then she broke a branch, put it in the water and tried to walk on it; she made a step in rather deep water and reached a fallen trunk on the other side. A young orangutan tried to cross the river by placing a small trunk upright in water, but the trunk sank almost completely. He tried to stand on the trunk, failed, fell in the water and did some hasty movements to reach the other side of the river. It is unclear if he touched the river bed or not. A third orangutan made a similar attempt with a longer trunk, with more success. He stood on the trunk, let it carefully fall in the water, stepped on it while letting himself fall in the water and reached the other side; the expression "mobile bridge-technique" to refer to this behaviour is proposed here.

Gorillas (*Gorilla gorilla*)

(a) Williamson et al (1988) reported on the problems that wild western lowland gorillas had when crossing marshes and streams in the Lopé reserve, Central Gabon: "They do not always use available log bridges, or take the most direct route" (Williamson et al. 1988, 30). **(b) A group of wild eastern gorillas refused to cross a stream less than 2 ft deep even when pursued by natives with spears or nets (Charles Cordier, pers. commun. in Schaller 1964, 103).** (c) Several times Africans showed George Schaller natural log bridges which gorillas regularly used to get from one bank to another (Schaller 1964, 103). **(d) Schaller found evidence at the Lugulu River that gorillas can reach the other side of a large river**

[51] *Unsere Affen – Tierportrait,* broadcast by Bayerischer Rundfunk, 1991.

only at the headwaters, using fallen trees forming natural bridges (Schaller 1964, 103). (e) At Mbeli Bai in northern Congo, a wild adult western gorilla female was observed using a trunk as a self-made bridge to cross a deep patch of swamp (Breuer et al. 2005). **(f) At the Cheyenne Mountain Zoo, USA, a new ape house was completed in 1966; it included a moated indoor system. The adult male gorilla 'Zulu' was very apprehensive of this moated area, and it took him nine months to venture into it (W.E.Meeker, pers. comm. to Cousins 1978).** (g) Golding described the behaviour of two gorillas after they were released in an exhibit at the University of Ibadan Zoo in Nigeria. Both gorillas were initially cautious. Soon after their self-confidence returned, they both climbed down into the moat and grasped the wire. Golding wrote:

> The reaction of the female was to retreat immediately, accompanied by a low whimper and frequent puzzled glances over her shoulder at the wire. She has since done her utmost to avoid contact with the wire and has certainly made no attempt whatsoever to cross from the inner moat section .[...] The reaction of the male, on receiving a shock, was to screw up his face and duck as though he had been attacked from above. He climbed back to the moat edge and moved around there, sitting down frequently and staring at the wire. After a few minutes he again went down and reached out and then withdrew his hand several times before his fingers eventually made contact with the wire and he received another shock. Again he ducked and retreated, and after a few more stares renewed his inspection of the compound. (Golding 1972, 74-75)

Bonobos (*Pan paniscus*)

(a) According to Kano [unpublished, mentioned in (Nishida *et al.* 1999, 160)], leaping quadrupedally – the usual pattern of crossing a stream via stepping stones as observed with wild chimpanzees (see, common chimpanzees (a) below) – is absent in bonobos of Wamba. **(b) According to Zanna Clay, bonobos at Lola ya Bonobo Sanctuary are often observed "using natural bridges to cross rivers, leaping over streams by jumping" (Zanna Clay, pers. comm.).**

Common chimpanzees (*Pan troglodytes*)

(a) "Adult males [chimpanzees] occasionally stand upright, swing their body back and forth in order to gain momentum, and then jump from a rock to another in upright posture when crossing a stream by using stepping stones" (Nishida *et al.* 1999, 160); see Fig. 3 of Van

Lawick-Goodall (1968) and in Quammen (2010, 58-59). **(b) Nishida reported that wild chimpanzees of Kasoje, Tanzania, „usually cross streams by (1) leaping quadrupedally, using stepping-stones or fallen-log bridges, (2) leaping bipedally while lifting both arms, or (3) climbing over arboreally (quadrupedal walk and/or brachiation). The second method is rather rare and was observed only with adult males. It seems that they try to avoid contact with water as much as possible in crossing streams. This situation is very similar to that observed at Gombe" (Nishida 1980, 200).** (c) A group of wild common chimpanzees crossed a 15-20 m wide river at Mahale by means of stepping stones. "Infants who usually walk on their own are carried on the belly of their mothers while crossing. A mother may have a newborn on her belly at the same time as she has her weaned infant on her back" (Nishida 1993, 25). **(d) Kortlandt reported on children up to six years riding on their mother's back to cross a brook. Some mothers with a child even made a 6 ft jump on two legs to cross the brook (Kortlandt 1962, 134).** (e) Jane Goodall wrote: „Chimpanzees normally jump a stream quadrupedally, although I have also seen them jump across bipedally as reported by Kortlandt (1962)"(Goodall 1965a, 439). **(f) Reynolds and Reynolds reported that wild chimpanzees in the Budongo forest normally did not come into contact with water when crossing swamps or streams. Instead, they used fallen branches as bridges, jumped over small streams and occasionally they crossed larger streams through the canopy (Reynolds & Reynolds 1965, 388).** (g) Chimpanzees at Chester Zoo are confined to islands surrounded by water. The water varies in depth from a few inches at the water's edge to about 3 ft in the centre of the waterway; the width varies from 14 ft to 17 ft. During all the time that the chimpanzees have been kept on islands at this zoo, they never tried to jump from one bank to another; most of them went only to the edge of the water (Mottershead 1960, 18). 'Compo', a male who was considered as very excitable, was released on one of the islands and found a large piece of concrete which had been left in the water between two of the islands. He took a running jump to land on the piece of concrete and jumped from there to the next island (Mottershead 1960, 19). **(h) "I did some work at Gombe National Park and noticed that the chimps did not even walk through a very shallow stream to cross, but instead jumped or went around" (Linda Brent, pers. comm.).** (i) "At Chimp Haven (Louisiana, USA), we have a large water moat in two of our outdoor habitats. It is about 60 ft across and about 8 ft deep in the middle. There is a very shallow part (about 1 ft deep and 10 ft wide) on the side where the chimpanzees have access. We did this so that if they wanted to wade and play in the water, they could. However,

none of our chimpanzees want anything to do with the water. In fact, a small inlet with water goes into one of the habitats and the chimpanzees would not wade through it – but instead went all the way around. We put a large rock in it so that they could cross. [...] Where I used to work, there was one chimpanzee who would actually get into pools and soak. I have also seen chimpanzees wade into the water at Ngamba Island Chimpanzee Sanctuary, Uganda, and also at Lion Country Safari, Florida" (Linda Brent, pers. comm.). **(j) Roger S. Fouts commented on his observations of chimpanzees' reactions to water:**

> It has been my experience that chimpanzees react to water in highly individualised ways. For example, Lucy was terrified of water and would cling to anyone in fear if you drove on a bridge over water. Likewise, Dar is very afraid of water and will not go near even small streams. On the other hand, Washoe enjoyed playing in water and actually once risked her own life in a moat while saving another chimpanzee [mentioned below in "Drowning individuals rescued by apes"]. Tatu is not afraid of water and we provide her with children's low swimming pools with warm soapy water she can play in. (Roger S. Fouts, pers. comm.)

(k) Golding wrote about the behaviour of an adult male and two adult females after they were released in an exhibit at the University of Ibadan Zoo in Nigeria. He described how the male chimpanzee grasped the wire about six times in the space of a few minutes. He continued: "From that day on, whatever the depth of the water, he has never attempted to leave the edge of the moat" (Golding 1972, 74). The females were more cautious in their initial explorations. When they finally touched the wire and received a shock, he recalled that "[t]hey, too, have never since attempted to leave the edge of the moat although one of them very occasionally stands with her feet and ankles in the shallow water at the edge itself, carefully holding on to the raised concrete kerb all the time" (Golding 1972, 74). Golding was convinced that "all three chimpanzees remember these unpleasant incidents of the first day" (Golding 1972, 74).

(l) Mottershead described the behaviour of chimpanzees towards the hot fire installed at the Chester Zoo after adult male 'Solomon' previously crossed the water moat:

> As a result of this escapade, it was felt that it would be wiser to install an electric wire in the centre of the waterway so that if a Chimpanzee attempted to cross, he would receive an unpleasant shock. The wire which was used was the same as that used for electric cattle-fencing. As soon as the wire was in position, Solomon went to investigate. He touched the wire and received a shock, looked at it and touched it again with the same result. Without further ado he went to each Chimpanzee in turn and apparently conveyed to them that this was

> something dangerous. "Elmer", the largest Chimpanzee then obtained a small twig from a willow tree, and whilst the other Chimps watched him, he cautiously touched the wire. Naturally he received a shock, and dropped the twig. Since that day the Chimpanzees have made no attempt to get into the water. (Mottershead 1960, 19-20)

Using artificial or natural floating items

For wading using floating devices see the section below on wading.

Orangutans (*Pongo pygmaeus*)

(a) Russon reported on several incidences of water contact in orangutans of a rehabilitation centre in Indonesia, including the use of floating objects as an aid to cross water bodies. One accidental use of a floating device was the use of a log as a 'boat' (Russon et al. 2010a; Russon et al. 2010b). In another instance, floating vegetation was intentionally used to travel on water (Russon *et al.* 2010b). **(b) At the rehabilitation centre Camp Leakey in Borneo, one adult female with an infant successfully used a boat, paddling with one hand (B.B.C./ Discovery Channel Co Production 2002).** (c) The Toronto Zoo has a moated area at the front of the Sumatran orangutan display. The orangutans learned to use floating objects to bridge the water. The keepers had to make holes in all bowls, barrels, and tubs, as one female tried to use these objects as boats and paddle over the moated area (she succeeded once) (Bev Carter, pers. comm.).(**d) An orangutan in a sanctuary in Borneo 'stole' a canoe and paddled on the river with it, using his hands as paddles. He reached a fishing net, took out a fish and ate it (Root 1987).** (e) A video shows an orangutan near Butik Lawang, Sumatra, occupying a boat lying on the shore and defending it vigorously against a guide who tried to chase him away (Anonymous 2009e)

Common chimpanzees (*Pan troglodytes*)

(a) In the sanctuary Chimfunshi in Zambia, a wall was built a short way into the river to impede the chimpanzees from walking around it. One day, the adult female 'Rita' got into a boat and paddled until she got around the wall, escaping successfully (Sheila Siddle, pers. comm.). **(b) On a man-made island, the young female 'Thelma' suddenly took a rowboat and pushed it into the pond with a powerful movement, jumping inside the boat next to the female 'Cindy'. Thelma's efforts were so strong that the boat was pushed toward the mainland (Fouts 1997, 141).** (c) One of the released chimpanzees of the H.E.L.P. (Habitat Ecologie et Liberté des Primates) sanctuary in the Republic of the Congo was 'specialized' in

stealing a boat. “I personally saw it crossing the river with the boat (a small boat) after pushing it from the ground.” (Yann Le Hellaye, pers. comm.). **(d) On July 15, 1999, Sylvia Corte, G. Duarte and F. Silveira, of the Universidad de la República, Uruguay, sent the following message to *Alloprimate*: “We are looking for information about zoo enclosures surrounded by water for baboons (*Papio hamadryas*). We want to know if water is a real barrier for the monkeys or if something else must be built between them and visitors. Would you recommend using water as a way of preventing the monkeys from escaping? If it is effective, how deep must it be and what are the advantages and disadvantages of this system? We also want to know if there could be any disease passed on by mosquitoes that could affect the health of monkeys (and people, of course)”; Duarte and Silveira in (Eckert *et al.* 1999). Linda Bamer posted the following response: “I worked at an “animal safari” place in which the animals were separated to some extent by moats. The chimps were on an island surrounded by water. One of them got hold of a tree limb and floated across to the lion section and was killed”; Bamer in Eckert et al. (1999).**

2. Different forms of wading

Since the wading techniques vary, this study reports on the results by separating the behavioural categories as follows: wading bipedally unsupported, wading bipedally with the aid of sticks or similar objects, wading bipedally with the aid of floating devices, and wading quadrupedally.

Wading bipedally (unsupported)

Gibbons (Hylobatidae)

A yellow-cheeked crested gibbon (*Nomascus gabriellae*) at the Saigon Zoo regularly waded in knee-deep water which surrounded the island where he was kept. From there he splashed water at the visitors (Geissmann *et al.* 2000, 25). Geissmann wrote: “When I was in Saigon, that gibbon was kept in an indoor cage, so I was not able to personally verify the reports of him wading in the water or splashing water at visitors. This gibbon was really exceptional, also in other respects of his behaviour” (Thomas Geissmann, pers. comm.).

Orangutans (*Pongo pygmaeus*)

(a) Bipedal wading in shallow streams is described as being common in wild orangutans where standing water is common and predators are absent, as in Borneo. Individuals of both

sexes and all age groups were observed wading at different sites (Van Schaik et al. 2006, 859). **(b) The wild-born adult male 'Kusai' was raised in a sanctuary. He was cautious but not reluctant to enter a river and cross it. He waded bipedally until the water reached armpit depth. From there he reached out for branches from the other side of the river and pulled himself across to the other side (Galdikas & Briggs 1990, 72, 73-75).** (c) In a documentary film on primates an adult male was shown wading bipedally in waist-deep water (Gérard Vienne 1989). **(d) Orangutans from a rehabilitation centre in Indonesia were repeatedly observed and photographed crossing shallow- and slow-water bodies by wading (Russon et al. 2010a; Schuster et al. 2008).** (e) In the Singapore Zoo an adult orangutan was observed wading in his moat (Ellis 1987). **(f) Crandall stated that water moats do not represent effective barriers in zoos to orangutans, because orangutans may learn to wade in shallow water. However, they appear to be helpless and therefore endangered beyond wading depth (Crandall 1971, 136).** (g) A female orangutan at the Toronto Zoo regularly wades up to chest depth in the water moat surrounding her island. There she tries to reach floating items of interest, but she seems to be very aware of how to get back to land safely (Bev Carter, pers. comm.). **(h) The juvenile male 'Suryia' wades regularly in the shallow part of a pool in a private zoo in Myrtle Beach (USA). He was introduced to water activities by humans (own observation; see more information on 'Suryia' in chapter 4.4).**

Gorillas (*Gorilla gorilla*)

(a) Still widely ignored is Harold C. Bingham's early report on indirect evidence of wild gorillas crossing streams: "Though the gorillas generally seemed to avoid water, there appeared to be no delay in plunging through a swollen mountain stream if there was sufficient necessity. At the place of fording there was a moderate current. The water was not deep enough to require swimming, but it was necessary for the observer to make use of submerged rocks to keep boot tops above water. The outstanding evidence of this crossing was the slippery banks up which the dripping animals had scrambled" (Bingham 1932, 60). It is not possible to infer from this statement whether the gorillas crossed the stream bipedally or quadrupedally. **(b) Williamson et al (1988) reported on wild western lowland gorillas in the Lopé reserve in Central Gabon. Knuckle prints in the sand along the river indicate that they regularly cross streams. Juveniles were observed crossing bipedally, while infants were carried on their mothers' back.** (c) Wild western lowland gorillas (*G. g.*

gorilla) regularly wade bipedally in the open, swampy clearings (bais) in the forest of northern Congo at Maya Bai (F. Magliocca, pers. comm.) and at Mbeli Bai (H.M. Buchanan-Smith, pers. comm.) where they feed on aquatic plants; for further data on this topic see following publications, videos and pictures: (video footage of wading gorillas in B.B.C./ Discovery Channel Co Production 2002; picture by Michael Nichols in Chadwick 1995; Doran-Sheehy et al. 2004; Magliocca & Gautier-Hion 2002; Nishihara 1995; Parnell & Buchanan-Smith 2001a; Parnell & Buchanan-Smith 2001b; Williamson et al. 1988). **(d) At the St. Louis Zoological Park the adult female 'Oka' and two younger animals, 'Mambo' and 'Sumaili', waded freely in shallow water when they pursued a purpose. However, they did not particularly seem to enjoy this activity (Crandall 1971).** (d) In a documentary[52], a family of western lowland gorillas in the Democratic Republic of Congo was filmed when entering a forest stream. A young gorilla is shown standing bipedally in very shallow water and playing with the water, splashing first with one, then with both hands.

Bonobos (*Pan paniscus*)

(a) Susman repeatedly observed tracks of wild bonobos along stream beds and in channel sands. It seemed that the animals waded in shallow rivers while feeding or travelling. Susman did not observe knuckle prints at the rivers, suggesting that bonobos, like common chimpanzees, "avoid getting their hands wet by assuming bipedal postures when crossing streams" (Susman 1984a, 373). **(b) Kano could not confirm the conclusions stated in (a), as he only observed quadrupedal wading in wild bonobos (Kano 1992, 126).** (c) Myers Thompson (2002, 67) described wild bonobos around a series of perennial pools in the Bososandja Refuge, Democratic Republic of the Congo, where they regularly fed on sub-aquatic vegetation. It was observed that adult individuals of both sexes used the pools; however, females with infants did not enter the water. In a quarter of all the encounters, bonobos showed bipedal locomotion while foraging in the pools. **(d) Several wild individuals were observed wading in chest-deep water (Gottfried Hohmann, pers. comm.).** (e) Several bonobos were observed and filmed wading bipedally in chest-deep water in the Lola ya Bonobo Sanctuary in the Democratic Republic of the Congo (Vanessa Woods and Zanna Clay, pers. comm.; see pictures in Anonymous (2012c). Working with bonobos in

[52] ***Mythos Kongo – Im Reich der Menschenaffen*, director Thomas Behrend, production Blue Planet Film; aired at ORF on 14.01.2014. See also** http://tvthek.orf.at/program/Universum/35429/Universum-Mythos-Kongo-Im-Reich-der-Menschenaffen/7326072/Universum/7353604**, assessed on 16 January 2014.**

the same sanctuary, Zanna Clay wrote that bonobos at Lola ya Bonobo Sanctuary interact with water extremely frequently – a behaviour which has been very well observed. She continued: "There are numerous individuals who will wade in water up to their chins. Even juveniles will cross water up to their shoulders". The bonobos' interactions with water are observed in connection with "play in water, cross water or fetch things out of water" (Zanna Clay, pers. comm.). **(f) Male bonobos 'Redy' and 'Vifijo' and female 'Dzeeta' were repeatedly observed wading bipedally in a zoo (Maarten De Rouck, pers. comm. in Kuliukas 2001, 23-24).** (g) During a study at Planckendael Wildlife Park, Belgium, eight individuals were observed wading bipedally for short moments (between 1 and 146 seconds). The wading was induced by visitors throwing food items into the water moat of the bonobos (Kuliukas 2001, 20-24). Adult female 'Hermien' with an infant clinging to her belly repeatedly entered the shallow water for one or two steps to retrieve the food item (Kuliukas 2011b; 2011c; 2011e). Similarly, the male bonobo 'Kidogo' was observed entering the water bipedally to retrieve a food item (Kuliukas 2011d). The results of this investigation were published by Kuliukas (2002). **(h) Vanessa Woods observed several bonobos wading bipedally, also in chest deep-water, at Lola ya Bonobo Sanctuary, Democratic Republic of the Congo (Vanessa Woods, pers. comm.).** (i) Zanna Clay, studying bonobos at the same sanctuary, wrote that they "interact with water extremely frequently". Although she did not publish on this topic, bonobos' intensive interaction with water has been very well observed there. She wrote: "There are numerous individuals who will wade in water up to their chins. Even juveniles will cross water up to their shoulders". They enter the water to "either play in water, cross water or fetch things out of water". They "walk and run bipedally through both shallow and deep water". They are often observed chasing bipedally through water. Although quadrupedal walking in water occurs, "bipedal walking is much more common". Wading is also used to escape from an aggressive individual: "One male stands in the lake to avoid aggression as the females are less courageous to go to the deeper areas, so he can make a quick escape. Males generally are braver and spend much more time in water than the females (Zanna Clay, pers. comm.); see also below report by Angus (1971) on chimpanzees entering water to escape from aggressive individuals. **(j) In the Democratic Republic of the Congo, certainly in a sanctuary, one bonobo was filmed while wading bipedally in water up to his armpits. One adult female carrying an infant was photographed standing bipedally in water up to her knees and bending down, taking water to her mouth with her hand. One individual was filmed wading bipedally in hip-deep water. One individual was**

photographed standing bipedally in knee-deep water. One individual was photographed standing upright in waist-deep water. Some of these records might show the same individual repeatedly (Anonymous 2011g).

Common chimpanzees (*Pan troglodytes*)

(a) Instances of wading individuals were regularly observed on islands off the southwest coast of the Republic of the Congo, in the chimpanzee rehabilitation programme H.E.L.P. (see Tutin *et al.* 2001). The areas where chimpanzees were released are liable to flooding and chimpanzees have to cross swamps to join feeding sites. Bipedal wading – often in chest-deep water – happens regularly during the wet season and was observed in all of the released chimpanzees (Yann Le Hellaye, pers. comm.). Karlowski (1996, 20) describes some particular wading behaviour in a group on one of the three islands at Conkouati, where chimpanzees were released and regularly fed. With exception of the dominant male 'Yombe', who has one leg amputated below the knee, the whole group runs into the water when the boat carrying the caretakers and the food arrives on the island. They hold their arms high "to keep as dry as possible." See pictures in Attenborough (2002, 297), and Penn (1996, 4). See film footage in B.B.C./Discovery Channel Co Production (2002).

(b) Angus (1971) reported from the semi-free ranging chimpanzee colony of 150 animals at the Aeormedical Research Laboratory, Holloman Air Force Base in New Mexico. In 1967, a group of chimpanzees was kept on an island surrounded by a water moat. Only two juvenile female chimpanzees ('Laveeta' and 'Annie') entered the moat, showing regularly wading, playing and splashing behaviour. They also entered the moat to escape from dominant animals (Angus 1971). (c) In the Chimfunshi sanctuary, Zambia, one enclosure was ten acres with a wall which reached the river. The wall continued into the river in order to prevent the chimpanzees walking around it. One female was observed entering the water up to her armpits and wading around the wall. Another individual waded to chest level, but not further (Sheila Siddle, pers. comm.). **(d) Victoria Horner observed one chimpanzee wading at waist level in a sanctuary in Uganda (Victoria Horner, pers. comm.).** (e) One young individual was filmed wading bipedally in very shallow water in a sanctuary (Gérard Vienne 1989). **(f) At the Vincennes Zoo in France it was observed that chimpanzees waded into water to chest level, but not further (Crandall 1971, 145).** (g) At the Lion Country Safari Zoo in West Palm Beach, USA, adult male 'Bashful' repeatedly

crossed the moat separating the different chimpanzee islands bipedally using a log under his arm-pit (see below "Wading bipedally with floating device"). One day, he got trapped in aquatic plants. In an attempt to free himself, he moved his arms in a similar way as a human swimming crawl stroke. After a long period of time, he managed to escape and reached the shore, completely exhausted. After this, he never tried to cross the water moat again (interview with Terry Wolf). **(h) Mottershead reported that most of the chimpanzees at the Chester Zoo will only go to the edge of the water moat, without entering it. The moat varies in depth from a few inches at the water's edge to about 3 ft in the centre; the moat width varies from 14 to 17 ft. The male 'Joe', raised as a pet by humans and used to being bathed every day, enjoyed wading in waist-deep water. One hot day in summer 1959, 'Joe' crossed the water and joined the chimpanzees on the next island. He was attacked by the other chimpanzees, managed to escape and wade back to his own island, followed by the male 'Solomon'. 'Joe' did not stop on his island but waded to the next island; from there he waded to the island used by the orangutans, and from there he climbed out into the zoo grounds, where he was caught by the zoo staff. Several weeks later, male 'Compo' jumped a wall over 12 ft. high in his indoor quarters and escaped through a ventilator. He was seen by the other chimpanzees on the islands and 'Solomon' immediately crossed the water moat to attack him. After a fight 'Compo' escaped, crossed some fields and was eventually shot (Mottershead 1960, 18-19).** (i) The adult male 'Dandy' at the Arnhem Zoo, The Netherlands, was the chimpanzee who dared to venture furthest into the water – always bipedally. "He usually did this during conflicts, to create a distance from his opponents, or to get at some food that was floating in the moat". In a later incident, one adult female crossed the moat by wading. "My hypothesis there was that she wanted to go look for her child, which had been taken away from her by zoo management" (Otto Adang, pers. comm.). **(j) The juvenile male 'Cooper' wades regularly in the shallow part of a private swimming pool in Malden, Missouri (USA) during hot summer days. 'Cooper' was raised by humans and is used to being bathed regularly (own observation; for more information on 'Cooper' see chapter 4.4).** (k) Bipedal gait in chimpanzees occurs when the ground is wet and cold (Köhler 1959, 278). **(l) A video shows a chimpanzee walking several metres bipedally through the wet grass in the Chimpanzee Sanctuary Northwest, Seattle, USA (Anonymous 2012f);** (m) A video shows a chimpanzee walking bipedally on snow at the Saint Louis Zoo (Anonymous 2010d). **(n) At Whipsnade Zoo in England, chimpanzees were once confined by a water moat 15-20 ft broad and**

about 2 ft deep in the middle. However, the animals discovered that they could escape by wading. As they did this repeatedly, this form of confinement had to be abandoned (Crandall 1971, 145). (o) One adult female entered the water in the Lion Country Safari Zoo, West Palm Beach (USA) and attacked the zoo director Terry Wolf, who wanted to bring her ill youngster to the veterinary clinic. In her anger she followed the boat by wading and had to be pushed back to the island with a long stick (interview with Terry Wolf).

Wading bipedally with stick or similar tool

Orangutans (*Pongo pygmaeus*)

(a) Galdikas reported on a wild female orangutan with an infant on her shoulders, wading through a pool on a foraging trip. A photograph of them shows that the mother uses a stick. Galdikas states that orangutans have surprisingly little fear of water (Galdikas 1980, 853). **(b) Russon reported on two individuals in a sanctuary in Indonesia who inserted a long stick into the water to test the water depth (Russon *et al.* 2010b).** (c) Sommer and Amman showed a photograph of a semi-upright orangutan crossing a ford with a stick. They assumed that the stick was used to test water depth and as support (Sommer & Amman 2007, 48-49); **(d) Another published photo shows the released male 'Rombé' in the Indonesian sanctuary of Tanjung Puting. He stands upright in knee-deep water, holding on tree trunks (Vienne & Collet 1989, 158-159).** (e) In a documentary film, one young and two adult orangutans are shown using a stick to cross the deeper part of a small river (Gérard Vienne 1989). **(f) Napier showed a photograph of the young male 'Jimmy' in a zoo in England, wading bipedally with a stick in his hand (Napier 1971a, 191).** (g) A video shows a female orangutan with a juvenile wading into a river. She first ventured in alone, using a stick to possibly test the depth of the water. She then retrieved a tree trunk from the water and ventured deeper with it into the river, still sounding the depth. Finally, she went back to the shore, took the juvenile on her shoulders and, with the aid of the trunk, crossed the river bipedally. The water was chest-deep and approximately 6-7 m wide. For the last 2 m she waded without the help of the trunk (Anonymous 2007c).

Gorillas (*Gorilla gorilla*)

One wild adult female gorilla was observed using a branch as a walking stick to test water depth and as an aid for her attempt to cross a pool of water at Mbeli Bai, Congo. This behaviour was described as the first documented tool use by wild gorillas. Also at Mbeli Bai,

another adult female was observed using a detached trunk from a small shrub as a stabilizer during food collection (Breuer *et al.* 2005).

Bonobos (*Pan paniscus*)

(a) In the Lola ya Bonobo Sanctuary, Democratic Republic of the Congo, Zanna Clay observed a male "using a stick to balance in deep water, while fetching a floating fruit" (Zanna Clay, pers. comm.). **(b) In the Democratic Republic of the Congo, certainly in a sanctuary, one bonobo was photographed wading bipedally in water up to his chest, holding a branch in one hand. It is unclear if he is using the branch as a support. One individual was photographed standing upright in hip-deep water, holding onto a tree trunk in the water (Anonymous 2011g).**

Wading bipedally with floating device

Common chimpanzees (*Pan troglodytes*)

In the Lion Country Safari Zoo in West Palm Beach (USA) the adult male 'Bashful' repeatedly crossed the moat separating the different chimpanzee islands using a log under his arm-pit. The log was about 4 ft long and 6 inches in diameter. To cross the moat 'Bashful' balanced bipedally on a ridge on the bottom of the moat left by the excavator. The moat reached a depth of about 8 ft in the middle, except where the ridge was and where the depth was around 6 ft. 'Bashful' advanced jumping along the ridge with the log under his arm, submerging time and again (interview with Terry Wolf) (see Fig. 4.2).

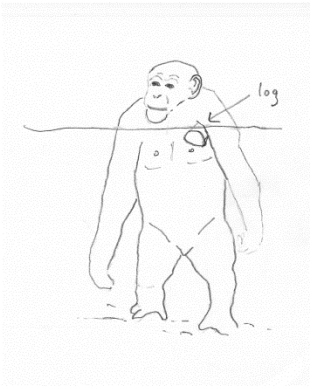


Figure 4.2 The male chimpanzee 'Bashful' wading bipedally using a log under his arm-pit and walking on a ridge on the bottom left by the excavator. The use of a floating device to support wading is unique in the present review. For a similar behaviour in humans, see below (chapter 5.4.3). Drawing by the author based on information by Terry Wolf.

Quadrupedal wading

Gorillas (*Gorilla gorilla*)

(a) Bingham reported on indirect evidence of movements by wild gorillas across streams: "Though the gorillas generally seemed to avoid water, there appeared to be no delay in plunging through a swollen mountain stream if there was sufficient necessity. At the place of fording there was a moderate current. The water was not deep enough to require swimming, but it was necessary for the observer to make use of submerged rocks to keep boot tops above water. The outstanding evidence of this crossing was the slippery banks up which the dripping animals had scrambled." It is unclear if the gorillas waded quadrupedally or bipedally (Bingham 1932). **(b) Several wild individuals (*G. g. gorilla*) were observed wading quadrupedally in the open, swampy clearings (bais) of a forest in northern Congo, e.g., at Maya Bai (F. Magliocca, pers. comm.) and at Mbeli Bai (Parnell & Buchanan-Smith 2001b).** (c) Terri Hunnicutt reported on one gorilla in a zoo that apparently loved water and used to wade into the water moats quadrupedally in chest-deep water (Terri Hunnicutt, pers. comm.). **(d) In a documentary53, a family of western lowland gorillas in the Democratic Republic of Congo was filmed when entering a forest stream. A silverback and a female entered the very shallow water of the stream walking quadrupedally. Another scene shows a female with a young on her back entering the stream quadrupedally. In another scene, an adult gorilla walked quadrupedally in shallow water, stopping to drink; afterwards this individual began to search something in water with the left hand, then began to walk quadrupedally and stopped where the water seemed to get deeper.**

Bonobos (*Pan paniscus*)

(a) In the large shallow swamps of the eastern Congo Basin several wild bonobos were observed for at least two consecutive months to regularly feed on aquatic plants in shoulder-deep water [Uehara, 1976]. **(b) Several wild individuals at Lomako Forest (DRC) were observed wading quadrupedally in very shallow water (Barbara Fruth (interviewed in De Waal & Lanting 1997, 80)).** (c) Several adults were filmed in a sanctuary in the Democratic Republic of the Congo wading quadrupedally in shallow water (pers. comm. and video footage by Vanessa Woods).

[53] ***Mythos Kongo – Im Reich der Menschenaffen*, director Thomas Behrend, production Blue Planet Film; aired at ORF on 14.01.2014. See also** http://tvthek.orf.at/program/Universum/35429/Universum-Mythos-Kongo-Im-Reich-der-Menschenaffen/7326072/Universum/7353604**, assessed on 16 January 2014.**

Common chimpanzees (*Pan troglodytes*)

(a) “When crossing a river, [wild] chimpanzees avoid contact with water and use stepping stones if available. If not, they walk quadrupedal in the river so long as the river is shallow” (Nishida *et al.* 1999, 179) **(b) Nishida reported on a behaviour by a chimpanzee of the Mahale Mountains, Tanzania, in October 1965. He heard the chimpanzee walking in a rapidly running stream (2.5 m wide and 40 cm deep). After the chimpanzee fled, he found remnants of a freshly eaten *Myrianthus* fruit on a small rock in the centre of the stream. “The chimpanzee surely waded the stream and ate the fruit on the rock on the way” (Nishida 1980, 195). In comparing the chimpanzees of Ksoje and of Gombe, he concludes: “Chimpanzees of Gombe rarely immerse even their fingers in water, even when crouching beside a stream to drink. There is a difference between the chimpanzees of Gombe and Ksoje in the degree of reluctance to make contact with water. But, wading is surely a very rare event even in chimpanzees of Kasoje and probably an idiosyncracy of a few individuals“(Nishida 1980, 200). Wading has been recorded twice in the M-group chimpanzees of Ksoje. An adult female of the K-group picked up a Saba fruit from a stream and ate it. Another adult female of the K-group immersed both legs and arms into running water in response to the pieces of sugar cane thrown into the river. No chimpanzees of Gombe have ever been recorded entering standing water. The experiment of throwing their desired food into water has not been done at Gombe, so it cannot be said how the Gombe chimpanzees would react to such an experiment. Chimpanzees of the M-group occasionally become at least partially wet while foraging for aquatic plants. Chimpanzees of the K-group seem to exploit the lakeshore environment much more extensively than Gombe chimpanzees (Nishida 1980, 205).** (c) In 1997, in the same region of the Mahale Mountains, Tanzania, the wild female ‘Sally‘ was repeatedly observed entering a stream and repeatedly picking up algae with one hand and putting it into her mouth. She advanced slowly into the water up to the knees and fed on a large amount of algae. Her arms were immersed into water up to the shoulders (Sakamaki 1998).

3. Swimming, preliminary forms of swimming and alleged swimming

Summary of deliberate swimming (confirmed by video footage)

Orangutans (*Pongo pygmaeus*)

(a) The juvenile male ‘Suryia’ swam on command between 2-12 m in a pool in a private zoo in Myrtle Beach (USA) (own observations; video footage by Bhagavan Antle and by the author; swimming in apes is described in detail in chapter 4.4. **(b) Professor emeritus Joseph Erwin, after reading the description on Suryia’s and Cooper’s swimming and diving behaviour (Bender & Bender 2013), wrote on an orangutan able to swim in a the Singapore Zoo (Joseph Erwin, personal communication); see details in chapter 4.3.5.**

Common chimpanzees (*Pan troglodytes*)

The 6-year-old male ‘Cooper’ swam repeatedly 2-3 m in a 2 m deep private swimming pool in Missouri, USA (video footage by Jill James; observations and video footage of preliminary attempts to swim by the author; swimming in apes is described in detail in chapter 4.4).

Summary of possible swimming or other form of underwater locomotion (not confirmed by video footage)

For details see chapter 4.3.5.

Common chimpanzees (*Pan troglodytes*)

(a) The adult female ‘Shasa’ swam regularly 2-3 m in a deep water moat in a sanctuary in Lubumbashi, Democratic Republic of the Congo (Roxane Chantereau, pers. comm.). **(b) In 2001, the male ‘Bilinga’ was observed on one of the three forested islands on the Conkouati Lagoon (sanctuary H.E.L.P.), Republic of the Congo, swimming a short distance in the proximity of branches (less than 1m away from the branches) when approaching the feeding boat (Yann Le Hellaye, pers. comm.).** (c) The young female ‘Barbara’ repeatedly crossed a 6 m wide moat under-water in the Lion Country Safari Zoo in West Palm Beach, USA (interview with Terry Wolf) (see Fig. 4.3).

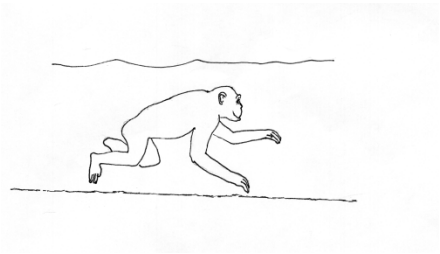


Figure 4.3 According to the information by Terry Wolf, the female chimpanzee Barbara repeatedly crossed a 6 m wide moat under-water in the Lion Country Safari Zoo in West Palm Beach, USA. Because she was fully submerged and the water had poor visibility, it is not known if she swam or crawled along the bottom. The gentle slope of the canal allowed her to wade about 2,5 m from the shores on both sides; and she was observed crossing the remaining 6 m under water. Drawing by the author based on information by Terry Wolf.

Preliminary stages of swimming

For details see chapter 4.3.4 on aquatic behaviours erroneously reported as swimming in the media.

Orangutans (*Pongo pygmaeus*)

Two individuals in a rehabilitation centre in Indonesia showed gliding or rudimentary paddling movements in three occasions over a short distance while playing in water (Russon *et al.* 2010b).

Gorillas (*Gorilla gorilla*)

In 1970, at the Ibadan Zoo, Nigeria, two gorillas began to interact intensively with water after they were released in a moated enclosure: „With the water up to their necks they were, of course, very buoyant and soon they began to propel themselves along in a sitting position - their faces just above water - by pushing their hands and feet against the underwater rails and moat bottom. […] Their prowess in the water developed rapidly and it was only a week or so before the male was able to launch himself with a kick from the moat bottom, travelling several feet in a horizontal ‘breast-stroke’ position with arms out straight in front of him, before slowing down and kicking out from the moat bottom again. He also launched himself by pulling with his hands against the underwater rails” (Golding 1972, 75).

Involuntary water contact (sporadically doubted as swimming in popular media)

Gibbons (Hylobatidae)

Thomas Geissmann reported on the observation of one adult gibbon pair (*H. muelleri* hybrids) kept on an island in the former DDR (East Germany) in 1988. He asked the director for permission to go close to the shore (the shore area was not open to the public) in order to take photos of the gibbons. The female got agitated when she saw him; she presented to him repeatedly. In such a context, he was unable to determine whether this behaviour was a friendly or aggressive (both explanations would have been possible in that situation). She ran along the shore opposite to his position, apparently trying to cross the pond, and finally jumped in the water. "She immediately climbed out of the water at the same spot where she jumped in. Water contact time was about two seconds. I am not sure whether she was able to reach the ground at the place where she jumped into the water or whether she actually swam for a second. In any case, she seemed to have cooled down after the bath and rejoined her climbing scaffolding. She did not come back to the shore and she did not present to me again" (Thomas Geissmann, pers. comm.).

Orangutans (*Pongo pygmaeus*)

One orangutan was described in a rehabilitation centre in Indonesia making a few paddling movements after momentary loss of upright posture during wading (Russon *et al.* 2010a).

This behaviour was reported in the media as an example of swimming behaviour; for the different (often erroneously or misleading) uses of term "swimming apes" in the media, internet, popular books and early scientific reports see chapter 4.3.4.

Common chimpanzees (*Pan troglodytes*)

The adult male 'Dandy' jumped from the enclosure into the water moat at the Arnhem Zoo, The Netherlands. Otto Adang reported:

> He did this at the point where over the years sand had accrued over the years and the moat was actually less wide than it used to be. Apparently he had speed and really jumped in an attempt to reach the other side. He did not quite manage that and I was told by my students who witnessed the event that he made a few arm movements and quickly reached the other side (the distance covered 'swimming' cannot have been more than 1,5 to 2 m). There he embraced the student standing there and shortly after climbed back into the enclosure via the wall. It

should be noted that Dandy had always been the chimp who dared to venture furthest into the water, but always standing upright on his legs. (Otto Adang, pers. comm.)

Alleged swimming

Results on alleged swimming and on aquatic behaviours erroneously reported as swimming in the media are reported separately in chapter 4.3.4.

4. Other forms of accidental or deliberate water contacts

Avoidance of rain

Gibbons (Hylobatidae)

Wild gibbons were observed stopping their movements and sitting quietly when it started to rain. Before continuing to travel, they engaged in very active grooming (Carpenter 1964a, 166).

Orangutans (*Pongo pygmaeus*)

(a) Van Schaik et al. (2006) describe common behaviours and behavioural novelties among wild orangutans from several observation sites in Indonesia. Behaviours related to rain (only observed in some areas) are: "Bunk nest: build a nest a short distance above the nest used for resting (during rain)", and "Hide under nest: seek shelter under nest for rain" (Van Schaik *et al.* 2006, 855). "Roof on nest in rain: a cover on the nest made by weaving together several twigs" and the use of branches as 'umbrellas' are both considered as to be common universals in wild orangutans" (Van Schaik *et al.* 2006, 862-863). **(b) A photograph shows a rehabilitant orangutan sitting in the rain, using a piece of carpeting as an umbrella in the Tanjung Puting National Park in Borneo (Schuster *et al.* 2008, 114).**

Gorillas (*Gorilla gorilla*)

(a) At the Audubon Zoological Garden in New Orleans, the 11-year-old western lowland male 'Scotty' spent long periods of time playing and probably also cooling off in the streams, small pool and moat in his enclosure. However, whenever it rained, both gorillas searched for shelter. "Getting wet from precipitation was clearly not comparable to soaking in the streams or the moat" (Brown *et al.* 1982, 248). **(b) Terri Hunnicutt reported that most of the gorillas she studied in the zoo do not like to be rained on (Terri Hunnicutt, pers. comm.).**

Common chimpanzees (*Pan troglodytes*)

(a) According to de Waal, chimpanzees "hate rain. In fact, they have a special expression, called their rain face of dirty face, put in while they are sheltering from a downpour. In fact, they have a special expression, called their rain face or dirty face, put on while they are sheltering from a downpour. With their lower lip stuck out and their upper teeth slightly bared, they are the picture of acute misery" (De Waal 1993, 184-185). **(b) Similarly, Reynolds and Reynolds confirmed the observations of the response of wild chimpanzees towards rain in the Budongo Forest. Light rain did not have a visible affect, but in heavy rain the animals would adopt an upright sitting position in the trees, with their heads resting on their arms folded in front of them (Reynolds & Reynolds 1965).** (c) Nishida reported that heavy rain would inhibit wild chimpanzees' activities. They would stop feeding or grooming if heavy rain began, and would wait until it stopped raining. However, chimpanzees do not necessarily search for shelter when it rains, but they were observed occasionally entering thickets. More commonly they were observed moving to the base of a tree to squat there. The posture assumed by chimpanzees during heavy rain is rather stereotyped: they sit in a squatting position, place each hand or forearm on each corresponding knee, bend the head down between both knees, and hunch the back. They often place the chin on the arm which is placed on the knee. These postures seem to be the same as observed at Gombe. Infants always rush to and are embraced by their mothers as soon as it begins to rain heavily. Uehara reported to Nishida that he once observed an old female breaking off a big branch with many leaves and using it like an umbrella during a heavy rain. At Gombe, only one chimpanzee was observed sheltering from the rain. Other authors have reported similar 'umbrella'-using behaviour for a chimpanzee of the Kasakati Basin (Nishida 1980). **(d) Victoria Horner reported from a sanctuary in Uganda: "I have never known a chimpanzee who likes rain" (Victoria Horner, pers. comm.).** (e) Robert and Ada Yerkes, according to their own observation for many months of four animals in the Yale Primate Laboratory, wrote: "All of them dislike […] to be wet by natural rainfall" (Yerkes & Yerkes 1945, 216). **(f) Although, in hot summer days, the 6-year-old male 'Cooper' spends hours playing, submerging, swimming and interacting with humans in a swimming pool, he does not like rain (interview with Jill James).**

Deliberated exposition to rain / rain dance

Bonobos (*Pan paniscus*)

Bonobos surprised Frans De Waal by their positive attitude towards rain, as he observed them "becoming playful on rainy days, wrestling and skidding about on the wet concrete" (De Waal 1993, 184).

Common chimpanzees (*Pan troglodytes*)

(a) A rare behaviour first described by Jane Goodall as a kind of "rain dance", is a highly excited behaviour shown by wild chimpanzees towards heavy rain or waterfalls (Lawick-Goodall 1971, 59; Van Lawick-Goodall 1968; Wallauer 2002). **(b) Sudden storms or heavy rain sometimes cause wild male chimpanzees to display. They slap the ground, run around with erect hair, shake or drag branches, stamp, rapidly climb on trees and so on. The 'rain dance' reported by Goodall seems to be a special case of synchronised display by several adult males. Only once was a young adult female observed showing such behaviour (Nishida 1980).** (c) One of the few reports of a chimpanzee that did not react negatively or extremely excited to rain was done by Roxane Chantereau from the sanctuary in Lubumbashi, Democratic Republic of the Congo, about the adult female 'Shasa': "Shasa doesn't mind standing outside in a pouring rain" (Roxane Chantereau, pers. comm.). **(d) J. A. van Hooff, writing on the chimpanzee consortium at the Arnhem Zoo, The Netherlands, described a spell of general excitement that occurred during a rain shower which resembled the "rain dance" described by Jane Goodall: "Animals started 'hooting'; some of them 'stamp-trotted' through the forest, swaying and dragging branches" (van Hooff 1973, 202).**

Deliberate or accidental head submersion (without drowning or near drowning)

Orangutans (*Pongo pygmaeus*)

(a) Some individuals in a rehabilitation centre in Indonesia were accidentally swamped by passing boats (Russon *et al.* 2010b). **(b) Anne Russon described the deliberate submersion of the body by orangutans, head included, under the surface of the water. She could not find a functional reason for this behaviour, but she assumed that it was a practice to re-gather objects sunken in deep water (Russon *et al.* 2010b).** (c) In the late 1970s, Gary Shapiro dived from a springboard in a sanctuary in Indonesian Borneo with the hand-reared

young female ‘Princess’ on his shoulders; both submerged completely (Anonymous 2012d). **(d) The young male ‘Suryia’ submerged repeatedly and deliberately (or on command) and swam under water in the pool of a private zoo in Myrtle Beach (USA) (own observation).** (e) The young female ‘Peanut’ in the Jungle Island Zoo in Miami (USA) laid on her back in a tub filled with water and repeatedly submerged her face (Linda Jacobs, pers. comm.; own observation).

Gorillas (*Gorilla gorilla*)

At the University of Ibadan Zoo in Nigeria, the male gorilla found out that he could get into the water moat, in spite of the electric wire, by carefully climbing between the underwater rails. To get his head on the other side of the wire he had to quickly submerge and pass under the wire, “grimacing furiously” on surfacing (Golding 1972).

Bonobos (*Pan paniscus*)

(a) Vanessa Woods, reporting on bonobos at Lola ya Bonobo Sanctuary, Democratic Republic of the Congo, wrote in December 2010: “We have never seen a bonobo put their head under the water” (Vanessa Woods, pers. comm.). **(b) In a popular book, Franz de Waal wrote: “I do not know if bonobos actually swim (which would make them unique among the apes), but they are known voluntarily to enter pools or moats, splash in the water, even dive completely under” (De Waal 1993, 185). When contacted about this passage he answered: “When I wrote ‘they are known to’ I meant this as claims that exist, I myself have never seen this”. He suggested contacting Zanna Clay, who studied bonobos’ behaviour in a sanctuary (see next paragraph) (Franz de Waal, pers. comm.).** (c) Zanna Clay, reporting on bonobos at Lola ya Bonobo Sanctuary, Democratic Republic of the Congo, wrote in December 2012: “I do not see bonobos regularly voluntarily submerging their heads; sometimes they have fallen in water and got their heads wet accidentally or jumped into water to avoid aggression” (Zanna Clay, pers. comm.).

Common chimpanzees (*Pan troglodytes*)

(a) Sylvia Jones and Sheila Siddle reported on repeated, deliberate partial and complete head submersions by three young females in the Chimfunshi sanctuary in Zambia (Sylvia Jones and Sheila Siddle, pers. comm.). **(b) The female ‘Kenya’ (born 1993) at the sanctuary “Center for Great Apes” in Florida (USA) “loved water-play and would often jump right into the**

hose-spray while the caregiver tried to wash down the outdoor habitats. When she would see someone with the hose, she'd get one of her "kiddie pools", carry it over to her caregiver, and wait for it to be filled with water. Then she would lie down in the water, twirl around in it, and even stick her entire head under water to blow bubbles! Today, as a young adult, Kenya is a bit more reserved in her play, but still loves to splash in water" (Anonymous 2012a). (c) In the Lion Country Safari Zoo in West Palm Beach (USA) the adult male 'Bashful' repeatedly crossed the moat separating the different chimpanzee islands using a log under his arm-pit. 'Bashful' advanced by jumping along the ridge with the log under his arm, submerging time and again (interview with Terry Wolf). **(d) In the Lion Country Safari Zoo, the adult female 'Barbara' escaped several times from her island crossing the moat by an unknown form of underwater locomotion. The gentle slope of the canal allowed 'Barbara' to wade about 2,5 m from the shores on both sides; and she was observed crossing the remaining 6 m under water. Because she was fully submerged and the water had poor visibility, it is not known if she swam or crawled along the bottom (Terry Wolf, pers. comm. and interview).** (e) The young male 'Cooper' kept by private owners in Malden, Missouri (USA) repeatedly and deliberately (or on command) submerged completely in a backyard swimming pool (own observation). **(f) Juveniles of M group of the Mahale National Park, Tanzania, were observed submerging their faces into water repeatedly in play in the river (Nishida *et al.* 1999) – a pattern limited to a few individuals of this group.**

Pouring water on the head

Bonobos (*Pan paniscus*)

An adult male was filmed in a sanctuary in the Democratic Republic of the Congo pouring water on his head and "washing his face", i.e., shaking his face laterally with the nose half-submerged (Vanessa Woods, pers. comm.).

Common chimpanzees (*Pan troglodytes*)

(a) The adult female 'Shasa' (for her "swimming" ability see chapter 4.3.5) in the sanctuary J.A.C.K. (Jeunes Animaux Confisqués au Katanga/Young animals confiscated in Katanga) in Lubumbashi, Democratic Republic of the Congo, goes regularly in water when the temperature is very high. She stays "maybe 15 to 20 minutes several times (3 to 4X) a day especially when the weather is very hot (September-October-November). During our winter

(April through July-August) she doesn't swim as it is too cold" (Roxane Chantereau, pers. comm.). **(b) Perhaps under the influence of 'Shasa' in the same sanctuary in Lubumbashi, Democratic Republic of the Congo, two other individuals began to enter the water when the weather was extremely hot. They are "no longer scared of water and walk in the pond until water reaches their hips. They don't go further or can sometimes sit in the water and put water over their heads" (Roxane Chantereau, pers. comm.).** (c) On hot days, some individuals seem extremely interested in interacting with a stream of flowing cool water at Yerkes Primate Research Center, e.g., wetting the tops of their heads, backs and arms (Victoria Horner, pers. comm.).

Allowing spraying water in the face

Orangutans (*Pongo pygmaeus*)

One adult male in the Jungle Island Zoo in Miami, USA, enjoyed having his face sprayed with a hose during hot summer days. Apparently, he did not mind if water was sprayed directly in his nose (own observation).

Common chimpanzees (*Pan troglodytes*)

The adult female 'Lilly' at the Johannesburg Zoo, South Africa, is very fond of getting water sprayed on her face; she is the only chimpanzee in her group to show this behaviour (Katherine Visser, pers. comm.).

'Washing' whole body or parts of the body /alleged 'washing' of the face

Gibbons (Hylobatidae)

(a) In 1833 Jardine reported on an ill female gibbon, which had to take a medical bath and apparently was delighted about it. When Jardine removed the gibbon from the bath, the gibbon would run back to the vessel and lie down again, until again made to move (Jardine 1833, 102). **(b) Jardine reported of an observation on wild siamangs by the animal collectors Diard and Duvancel. They reported that the siamang mothers were very caring about their offspring and that they would carry them to streams to wash their faces, wipe and dry them in the most careful manner (Jardine 1833, 106).** (c) Similarly, Forbes (1897, 151) reported that siamang mothers would wash the faces of their babies. (He did not quote any source, but it is probable that he was relating to the above-mentioned statement by Jardine). **(d) Yerkes and Yerkes do not believe this and interpret the**

observation as drinking behaviour by the mother, during which she bends over the water with her baby clinging on her belly, wets her hand and licks the water from her hand. According to Yerkes and Yerkes this could look like washing the baby (Yerkes & Yerkes 1945, 59).

Orangutans (*Pongo pygmaeus*)

(a) Russon reported on rehabilitant orangutans from Kaja Island, Central Kalimantan, Indonesia washing their faces or arms with water from a tree hole (Russon *et al.* 2010b). **(b) A rehabilitant orangutan from Kaja Island, Central Kalimantan, Indonesia, was photographed while having a bath in a tub (Schuster *et al.* 2008, 124).** (c) Alfred R. Wallace raised a one-month-old orangutan; he described its reaction towards water during bathing: "I soon found it necessary to wash the little mias [orangutan] as well. After I had done so a few times, it came to like the operation, and as soon as it was dirty would begin crying, and not leave off till I took it out and carried it to the spout, when it immediately became quiet, although it would wince a little at the first rush of the cold water and make ridiculously wry faces while the stream was running over its head" (Wallace 1869, 54). **(d) Harrisson wrote that an orangutan mother at the Dresden Zoo in Germany "kept her baby clean – using either water or her urine – to wash its fur where necessary. I treated [the male orangutan] Ossy similarly, using lukewarm water, but often gave him a full bath when the weather was warm and dry. He liked this very much, as also having his long, shiny hair combed" (Harrisson 1987, 127).** (e) A video showed two young orphan orangutans being washed by caretakers in a sanctuary in Borneo (Anonymous 2010b). **(f) A video showed a young orphan orangutan washing himself frenetically with soap in the sanctuary of Biruté Galdikas in Borneo (Fellmann 2011a).** (g) A video showed a young orphan orangutan being washed by a caretaker in the sanctuary of Biruté Galdikas in Borneo (Fellmann 2011b). **(h) An orangutan (possibly Gypsy, a 56-year-old female at the Tama Zoo in Tokyo, Japan) was filmed using a towel to wash her face. She repeatedly dipped the towel into the water, wrung it out and washed her face or the border of the fountain with it. A young individual approached and observed her, trying to imitate the movements (Anonymous 2011f).**

Gorillas (*Gorilla gorilla*)

At the Audubon Zoological Garden in New Orleans, the 11-year-old western lowland male 'Scotty' would often make 'washing movements' while sitting in the moat, sometimes employing leaves in the process (Brown *et al.* 1982).

Bonobos (*Pan paniscus*)

One adult male was filmed when "washing" his face at Lola ya Bonobo Sanctuary, Democratic Republic of the Congo (Woods 2009).

Common chimpanzees (*Pan troglodytes*)

(a) In the Chimfunshi sanctuary in Zambia, the female 'Alice' was observed taking handfuls of water up to her face and wiping her face with it (Sylvia Jones and Sheila Siddle, pers. comm.). **(b) Cherry Kearton described the young hand-raised male 'Toto' trying to imitate him by brushing the teeth, washing the face, hands and feet in a tub (Kearton 1965, 7-9).** (c) The young female 'Viki' was raised by humans in an experiment of language learning. Viki was regularly bathed and learned to enjoy this:

> Now during her bath, Viki began paddling her hands in the water. Then she hung onto the edge of the tub and kicked with her feet. When I held her under the tummy, as children are held for swimming lessons, she made the proper motions. I then took my hands away, and to my amazement, she remained completely suspended for five seconds before her feet sought bottom. She seemed delighted. Although she coughed and sputtered from the water in her nose, she always laughed and went back for more. Once again, we almost had cause to regret her latest achievement. She became too fond of water that one wintry day, she ran away to Mrs. Clarke's and jumped into the ice-cold fish pond. (Hayes 1952, 130)

(d) Reynolds reported about the young female 'Gua', another chimpanzee raised by humans. 'Gua' did not like to be bathed in the beginning, but with the time, she learned to enjoy it. At the age of ten months she also learned to enter the pool (Reynolds 1967, 187). (e) The young male 'Snookie', a chimpanzee raised by humans, was described as loving to play with a cup to dribble water into a tub. He also used a rag to wash his face (Noell 1979, 40). **(f) The hand raised male 'Cooper' was regularly washed and bathed in a bath tub by his owners in Malden, Missouri (USA), where he also learned to submerge (interview with Jill James).**

Sitting or lying in water without head submersion

Orangutans (*Pongo pygmaeus*)

(a) Russon described how some orangutans in a sanctuary in Indonesia hid from opponents underwater: they went into deep water and ducked down so that only the top of the head was visible (Russon *et al.* 2010b, 291). **(b) In a private zoo in Myrtle Beach (USA) three young individuals were observed sitting and playing in shallow water in a children's wading pool (own observation).**

Gorillas (*Gorilla gorilla*)

(a) In Equatorial Guinea, guides of the Fang tribe told J. Sabater Pi that they had many times seen wild lowland gorillas 'bathing' in forest streams (Groves & Sabater Pi 1985); it was not specified what 'bathing' means. Usually, gorillas' interaction with water is described in connection with bais; however, a documentary[54] showed a family of western lowland gorillas in the Democratic Republic of Congo entering a forest stream, with adults walking quadrupedally, drinking and young playing (but not 'bathing' in the sense of sitting in water or submerging the body in water deeper than around knee depth). **(b) The two 11-year-old western lowland gorillas 'Scotty' (male) and 'Molly' (female) at the Audubon Zoological Garden in New Orleans, Louisiana, were observed during their interactions with water. Both were captured in the wild as infants and subsequently raised together at the zoo. In their enclosure, a waterfall fed a series of small streams which emptied into a large moat. Directly under the waterfall was a small pool. Most observations concerned 'Scotty', as 'Molly' entered the small pool and streams (never the moat) only for short periods during three days late in the study. On the few occasions she entered the water, the male immediately chased her out. Scotty spent more time in the water of the small pool and streams than in the large moat. While in water he usually maintained a sitting position, only occasionally walking up and down the streams. It seemed that a high air humidity was an important factor for ‚Scotty' to enter water (Brown *et al.* 1982).** (c) The adult male 'Phil' at the St. Louis Zoo learned to leap freely into 4 ft deep water up to his neck, after which he sat quietly on the bottom of his moat (information given by George P. Vierheller to Crandall 1971, 164-165).

[54] ***Mythos Kongo – Im Reich der Menschenaffen*, director Thomas Behrend, production Blue Planet Film; aired at ORF on 14.01.2014. See also** http://tvthek.orf.at/program/Universum/35429/Universum-Mythos-Kongo-Im-Reich-der-Menschenaffen/7326072/Universum/7353604**, assessed on 16 January 2014.**

Bonobos (*Pan paniscus*)

(a) In the large swamp of the eastern Congo Basin, wild individuals were observed copulating in ventro-ventral position in shallow water, with the females getting completely wet (Uehara 1976). **(b) According to Vanessa Woods, one adult male at Lola ya Bonobo Sanctuary, Democratic Republic of the Congo, was filmed while sitting and lying down in shallow water (Woods 2009).** (c) According to Zanna Clay working at the same sanctuary, bonobos there are often observed "wallowing, soaking on their backs in water" (Zanna Clay, pers. comm.). She assumes that water is used for thermoregulatory purposes: "Males often spend time in water to cool down in the hot periods, females less so but also will do this sometimes" (Zanna Clay, pers. comm.).

Common chimpanzees (*Pan troglodytes*)

(a) At Fongoli, in Senegal, wild males, females and juveniles like to spend time in ponds filled up with rain water during hot days (Pruetz & Bertolani 2009), probably for thermoregulatory purposes. Sometimes they also lie down on the riverbed of a small stream. Some individuals "do submerge past their shoulders on occasion, but I have yet to see anyone go under, and they almost always anchor themselves when they are in the pools - holding onto vines or the side of the rock pool" (Jill Pruetz, pers. comm.). "They can stay several minutes (30-45') into the water; sometimes they do some grooming or just sit there" (Paco Bertolani, pers. comm.). This behaviour is documented in video footage. The scene was filmed at the Sakoto pool, created by the first heavy rain of the season. First, an adult male appeared and carefully entered into it. A further five males followed him. Hanging constantly onto vines and crouching, they stood immersed up to their chests, some apparently drinking. Later, the oldest male of the group entered the pool after the first chimpanzees had left it. After he left the pool, females with their offspring came at the pool; one young chimpanzee, hanging on vines, seemed to watch and play with his reflection in the water (Eckstrom 2012). **(b) Nishida reports on the wild female 'Tula' of the Mahale forest, standing on all fours near a pool in a running stream, trying to bail out the water with one hand. "Then she immersed herself in the water, splashed it and tried to uproot a submerged old buttress of a tree" (Nishida 1993, 24).** (c) In H.E.L.P.'s sanctuary, in the Republic of the Congo, chimpanzees are probably also using water for thermoregulatory purposes in hot days. "That is pretty sure, at least on rehabilitation islands where individuals go down in the water for some seconds and

go back on mangrove" (Yann Le Hellaye, pers. comm.). **(d) Several young chimpanzees in a sanctuary in Uganda were observed during hot days immersing themselves in a bucket of rain water up to their necks and sitting there for several minutes (Victoria Horner, pers. comm.).** (e) In the Lion Country Safari Zoo in West Palm Beach (USA), during hot days several adults sit regularly for several minutes in a water moat, with the water reaching chest level. Some individuals go to the water just for a few seconds and then go back to land (interview with Terry Wolf; own observation with video footage). **(f) Marianne Holtkötter, from the Wilhelma Zoological-botanic gardens in Stuttgart, Germany, wrote that the apes in this zoo (species?) only have pools with a water depth of 20-30 cm. It is used by the different species in a very individual way, such as bathing the feet, sitting in it or playing (Marianne Holtkötter, pers. comm.).** (g) Simone Peters from the Zoo Leipzig, Germany, wrote that the apes in their zoos enter into the water moat but not further than knee-deep water. At the time she replied, the zoo only had a single gibbon. However, their past experience showed that gibbons usually did not enter the water (Simone Peters, pers. comm.). **(h) In Missouri, USA, on hot days, the young hand-reared male 'Cooper' regularly sits on the stairs of a private swimming pool with water up to his chest (own observation).**

'Washing' food or objects

Orangutans (*Pongo pygmaeus*)

(a) Biruté Galdikas reported from the sanctuary Camp Leakey in Borneo, that the adolescent female 'Cempaka' liked to grab rags and soap and to wash them in a receptacle with water. She probably imitated her former owners (Galdikas-Brindamour 1975). **(b) A rehabilitant orangutan of Kaja Island, Central Kalimantan, Indonesia, 'washed' towels as he has seen humans do (Schuster *et al.* 2008, picture on p. 119).**

Gorillas (*Gorilla gorilla*)

Gorilla male 'Kiki' in the Woodland Park zoo, Seattle, had a mild attack of diarrhoea and made "a small mess on a rock. He went to the stream and scooped up water to wash off the spot"(Cousins 1990, 263).

Bonobos (*Pan paniscus*)

(a) Several wild bonobos from Lilungu (Ikela), Zaire, were repeatedly observed washing food (e.g. earthworms, aquatic plants or muddy roots) before eating them (Bermejo et al. 1994). **(b)**

Zanna Clay, reporting on bonobos at Lola ya Bonobo Sanctuary, Democratic Republic of the Congo, observed individuals washing objects in water, most probably for play; sometimes vegetables are also washed (Zanna Clay, pers. comm.).

Common chimpanzees (*Pan troglodytes*)

(a) The wild adult male 'Musa' in the Mahale forest in Tanzania was seen to 'wash' the pelt of a colobus monkey in a stream, by submerging it repeatedly and shaking it in the water. He brought it out, stamped his feet on the rock repeatedly in a bipedal posture and repeated the whole process several times. After this treatment, Musa nibbled the skin. According to Nishida, Musa possibly wanted to clean the skin or tender it (Nishida 1993, 24). **(b) Cherry Kearton (1925) (reprinted in 1938) wrote about the young captive male chimpanzee 'Toto' "[W]e saw a group of native 'boys' sitting on the ground, washing clothes. Taking his place in the circle, accepted apparently without question as an additional helper and hard at work, sat Toto. He was entirely absorbed in his task, washing a cloth with soap in a bowl of water, wringing it out in exact imitation of the way the natives worked, then wetting it with a cupful of clean water and wringing it out again" (Kearton 1938, 77) .** (c) Sheila Siddle reports from the sanctuary Chimfunshi in Zambia: "[Chimpanzees in captivity often wash] their hands or their bottle or sometimes even a fruit if they think it is not quite right. They certainly know what water is for and how to use it. When we had chimps living in the house with us when they were babies I have even seen them copy me and rub their hands with soap. We have one chimp called 'Milla' and she has been given a blanket. Every now and then she will put the blanket in her very big water dish and look like she is 'washing' it. It then gets hung on the shelf in the night cage until it is dry" (interview with Sheila Siddle). **(d) A juvenile chimpanzee at the Johannesburg zoo playfully 'washed' a dead bird in a creek crossing the chimpanzee exhibit (own observations).** (e) Anna Mae Noel wrote about the young male 'Snookie', a chimpanzee raised by humans:

> [Snookie] loved nothing better than a basin or tubful and either a rag or a cup with which to dribble the water back into the tub. I've often wondered if he was merely admiring the cascade, or was some inventive idea locked away in his mind because of our language barrier? With these simple "toys" he could amuse himself for hours on end. He would use the rag to wash his face as he had so often seen us do. But his favorite way to handle it was to wring the rag out, over and over. First he would dip the rag into the water, hold it aloft watching the water run off into the tub, and then wring it carefully, looking at it as if this was a great

> mystery he alone was called upon to solve. He would do this literally hundreds of times. Sometimes he would vary the procedure by rubbing the soap on the wet rag and making billowy suds in the tub. He would even try to eat the suds. Then back to the rag wringing bit. We never figured out why this amused him so much, and if we wanted to remove the tub, he would throw a temper tantrum. It was such a consuming pastime to him he would refuse to let the tub out of his sight. Even when we took him into our trailer (rarely) the first place he went for was the wash basin in our bedroom, where I turned on a sink full of warm water, gave him a rag and a piece of soap and then we could relax for at least an hour. (Noell 1979, 40-41)

(f) Wolfgang Köhler describes young female 'Nueva' playing water-games (see also below "Playing in water"): "She also used her bread – for which she did not care very much – in this water game; she dipped and soaked it and then sucked the water from it; dipped and soaked again, and so forth" (Köhler 1959).

Playing in water, splash display, interaction with aquatic animals, and other uses of water

Orangutans (*Pongo pygmaeus*)

(a) In Borneo especially, where there is still or slow running water and no predators, wild orangutans may come to the ground and wade in shallow water. At least three individuals (an adolescent female, an adult female and an adult male) at Tuanan were observed playing in water by splashing it with their hands. They got thoroughly wet and even dipped completely under the water's surface. Van Schaik considered this behaviour as an innovation at this site (Van Schaik *et al.* 2006, 859). **(b) Russon confirmed that water play is rare in wild orangutans but common in rehabilitants and in captives. As water can be dangerous to wild orangutans, maternal guidance could constrain opportunities of young animals to explore it. In rehabilitants, where such constraints are absent, water play is rapidly acquired if access to ground water is possible. Furthermore, at some sites rehabilitants may see water use in familiar humans, so social influences cannot be ruled out (Russon *et al.* 2010b).** (c) In his description of play behaviour in animals, Brown described (showing a photo) an orangutan in Sumatra hanging upside down from a tree to drink and to play with the water (Brown 1994, 2). **(d) Schuster et al. succinctly described and showed 17 photos of a five-year-old male orangutan at the Ragunan Zoo in Jakarta "playing and fighting with the spout of water coming out of a tap that is normally switched off" (Schuster *et al.* 2008,114, pictures on pp. 115-119).** (e) In T.I.G.E.R.S. (The Institute of Greatly Endangered and Rare Species), a private zoo in Myrtle Beach, USA, Bhagavan Antle described juvenile

orangutans being fascinated while playing with soap bubbles (interview with Bhagavan Antle). **(f) Willie Smits, head of the Borneo Orangutan Survival Foundation, describes how orangutans in rehabilitation sites "enjoyed playing with soap bubbles and seemed fascinated by their opalescent and transient beauty. They loved water games"(Smits in Schuster *et al.* 2008, 128).** (g) In a private zoo in Myrtle Beach (USA), the author and Nicole Bender observed and filmed three individuals playing in a paddling pool and with a garden hose. They repeatedly poured water over their heads (own observations). **(h) Bev Carter, once the keeper at the Toronto Zoo, Canada, reported on orangutans at the Toronto Zoo which "will sit at the edge of the moat and try to redirect the flow of water with their hands or by using sticks, to bring objects closer to where they're sitting" (Bev Carter, pers. comm.).** (i) Bev Carter reported on a female orangutan at the Toronto Zoo that "has discovered that if she wets a bed sheet and then covers herself and has one end draped over the air vent, she can have instant air conditioning. Another female orangutan will fill a pail with water from the moat and then use fabric to wash the windows in the exhibit. She then uses her forearm to try and squeegee the excess water off the window" (Bev Carter, pers. comm.). **(j) Bev Carter reported on juvenile orangutans at the Toronto Zoo that "use water as a means of getting a reaction from their keepers. They'll get a mouthful of water from their auto waterer and wait until the keeper is distracted and then they'll spray the water on the keeper and enjoy the reaction" (Bev Carter, pers. comm.).** (k) A young female at the Jungle Island Zoo in Miami, USA, took water in her mouth to spit through the bars repeatedly on researchers (own observation). **(l) In the Zoo of Basel, Switzerland, an orangutan female used to make a "mud bath" in a tub (1x1m and *ca* 30 cm deep) out of water, paper, hay and straw, and to relish splashing around in it (Jakob Huber, pers. comm.).** (m) The 56-year-old female orangutan 'Gypsy' was filmed at the Tama Zoo in Tokyo, Japan, while playing with a small water fountain. She repeatedly touched the water with her hands and her mouth. She stepped on the fountain opening with one foot, almost stopping the water flow. She inserted one finger into the fountain opening, producing a much higher water stream. This attracted another orangutan, which was on a platform above the fountain, and touched the now high water stream with one hand. 'Gypsy' later took a plastic basin and filled it with water, which she emptied on the grass. She also filled her mouth with water and spat it into the basin (Anonymous 2011d). **(n) An orangutan in a zoo carried a stick to the water moat. The level of the water was about 1 m below the board of the moat. The orangutan used the stick to try to retrieve floating leaves on the water**

(Anonymous 2011c). (o) The orangutan 'Kinda' at the Houston Zoo, USA, approached the shore of a fish pond. A large orange fish (possibly a carp) approached the orangutan (perhaps in the expectation of being fed); the orangutan 'chased' the fish away with one hand. The fish approached a second time and splashed water at the orangutan, who fled terrified (Anonymous 2011a).

Gorillas (*Gorilla gorilla*)

(a) Wild western lowland gorillas (*G. gorilla gorilla*) were observed using water to generate spectacular splash displays in swampy, open areas, mostly by silverbacks in an agonistic context (Parnell & Buchanan-Smith 2001a; 2001b). **(b) At the Audubon Zoological Garden in New Orleans, the 11-year-old western lowland male 'Scotty' frequently splashed the water and once used a stick for this purpose. Furthermore, when he entered the large moat, (0.5 m in the deepest part) "he usually walked from one end to the other, [and] splashed in the direction of the people gathered on the pathway" (Brown *et al.* 1982, 246).** (c) Robert Golding described the behaviour of a pair of young lowland gorillas towards water at the Ibadan Zoo, Nigeria, after they were first released in the moated enclosure in 1970. (Golding's observations are reported in detail in chapter 4.3.4). Within a few days of having access to the moat, both animals began to sit on the bottom of the moat with the water up to their chins, always keeping their heads above water. They began to beat the water with their hands, delighted by the variety of noises that could be produced through the splashing. They frequently stood up, with water pouring off their bodies, beating their chests violently and then submerged again. "Both animals soon learned to run across the compound and either leap diagonally into the water in a tremendous belly-flop or twist around at the last minute and plunge in backwards, all the time being careful not to submerge their faces. They took turns in chasing each other along the edge of the moat, the one behind attempting to push the other into the water" (Golding 1972, 75). Golding described the gorillas enjoying contact with water even before they had access to the moat: "On hot days they loved nothing more than to be drenched with water from the hose pipe, becoming very excited and boisterous in the process" (Golding 1972, 71). **(d) At the St Louis Zoo, the adult male 'Phil' became accustomed to water-play at an early age. He learned to leap freely into water 4 ft deep which rose up to his neck when he sat quietly on the bottom (Cousins 1978).** (e) C. R. Carpenter reported on the male mountain gorillas 'Ingagi' and 'Mbongo' (both eight years old) at the San Diego Zoological Garden. Within the outside cage there was a pool of water

large enough for the animals to bathe in. On one event recorded in July 20, 1934, Carpenter observed: “Ingagi played for many minutes in the pool of water. At the first he dipped the water up in one hand and let it run into the other. Later he slapped most of the water from the pool. Then he took water into his mouth and let it run out again” (Carpenter 1964b,113). He noted that water is one of the apes' most preferred playthings. For instance, he described how both gorillas were fascinated by running water from a hose: “Whenever possible, they would come to the hose and open their mouth for the stream to pour in. The animals competed for this stream as they would compete for food” (Carpenter 1964b, 113). Another quite common behaviour was a type of skating or sliding play on the wet floor. They did not skate with their legs and feet, but with their arms and hands: “With their arms stiffened and held forward at an angle from their shoulders and with their knuckles in contact with the cement, while running with their feet, they would slide their hands from one end of the cage to the other and back again until they became fatigued. Typically this was done at a trot or rapid run” (Carpenter 1964b, 113). Carpenter considered the water use for purpose of drinking, playing and bathing as an essential factor for the gorillas: “In fact, it seems evident that constant access to a plentiful supply of water is one of the important factors in the success of the San Diego Zoological Gardens in keeping these animals in captivity healthy, content and growing normally” (Carpenter 1964b, 112). **(f)**

At the Twycross Zoo near the village of Twycross in Leicestershire, England, the young male gorilla ‘Joe’ was filmed taking a bath in a tub; a chimpanzee ran about the side of the bath and played with him. ‘Joe’ splashed several times with the hands, while sitting on the bottom of the tub; he also splashed vigorously with arms and legs while lying on his back (British Pathé (producer) 1967). According to Don Cousins, years later, ‘Joe’ continued to show a strong attraction to water, playing in a pool of his indoor quarters. He described that a soap solution is often added to the water in the bathing tub, and Joe creates a mass of lather out of this when he drums vigorously with his great arms on the surface of the water; the other gorillas kept their distance from the water (Cousins 1978). (g) An adult male gorilla at the Pittsburgh Zoo, USA, entered into shallow water quadrupedally on a hot August day. He lay on the side and rolled over his back, stood up on all fours and waded quadrupedally (Anonymous 2008a). **(h) In a documentary[55], a family of**

[55] ***Mythos Kongo – Im Reich der Menschenaffen*, director Thomas Behrend, production Blue Planet Film; aired at ORF on 14.01.2014. See also** http://tvthek.orf.at/program/Universum/35429/Universum-Mythos-Kongo-Im-Reich-der-Menschenaffen/7326072/Universum/7353604**, assessed on 16 January 2014.**

western lowland gorillas in the Democratic Republic of Congo was filmed when entering a forest stream. A young gorilla is shown standing bipedally in very shallow water and playing with the water, splashing first with one, then with both hands. (i) The Huston Zoo's gorilla habitat display opened in December, 1973 and was evaluated by Richard Quick in 1976. The terrace floor surface is divided by a flowing stream with five shallow pools bordered by concrete boulders. The two young gorillas show vivid activities. „The male especially is fond of making spectacular splashes by dropping six to eight feet from the swinging wine into the 18 inch deep pool. Shallow water for play is a must for any new gorilla enclosure“ (Quick 1976, 13-16). **(j) Terri Hunnicutt observed apes playing in water provided for them in shallow paddling pools or horse feeding troughs. “I have never worked at a facility that had water moats deeper than about 12 inches. The apes would wade into those at the edge and splash around but not often and typically it would be the kids, not the older apes. […] Almost all of the apes I have ever worked with loved playing in a hose mister or sprinkler, and/or having a caregiver hold the hose while they played in the stream. A lot of times they seem to enjoy feeling the stream on their hands, much as humans do” (Terri Hunnicutt, pers. comm.).** (k) Kris Hern, animal training manager at the Twycross Zoo near the village of Twycross in Leicestershire, England, observed: “The gorillas also have a bath area and I knew of one gorilla that would sit on the edge of the bath and splash his legs in it (kicking the water)” (Kris Hern, pers. comm.).

Bonobos (*Pan paniscus*)

(a) Wild adults (but not adult females carrying infants) regularly gather to feed on sub-aquatic vegetation around a series of perennial pools in the Bososandja Refuge, Democratic Republic of the Congo. In the meantime, immature individuals “remained on the shore, playing only in the shallow waters that could be reached with an extended hand, sometimes supported by holding onto vegetation to lean out over the water” (Myers Thompson 2002, 67); **(b) At Lilungu (Ikela), Democratic Republic of the Congo, a young male was observed playing in water in the wild (Bermejo *et al.* 1994).** (c) After being charged by the adult male ‘Tatango’ at Lola ya Bonobo Sanctuary, Democratic Republic of the Congo, adult male ‘Kikwit’ “runs down to the lake and is so upset, he starts hitting his own reflection in the water” (Woods 2010, between pp. 152-153, with picture). **(d) Kris Hern, animal training manager at the Twycross Zoo near the village of Twycross in Leicestershire, England, observed: “Bonobos are more the ones that interact with the water from their baths. The**

male 'Keke' likes to sit on the edge of the bath and put his legs in from time to time (the water is cold) they tend to splash with this more, especially the juveniles" (Kris Hern, pers. comm.). (e) Nishida et al., stated that the behaviour described as putting "an object into water without releasing it [dunk]" is "[a]bsent in the [wild] bonobos" (Nishida *et al.* 1999). **(f) According to Zanna Clay, bonobos at Lola ya Bonobo Sanctuary, Democratic Republic of the Congo, interact intensively with water. They play with water in artificial basins as well as in lakes, streams and ponds. For instance, they are observed (1) sticking sticks and leaves in water to play with, (2) filling their own plastic bottles from streams to drink with and play with, (3) chasing each other (Zanna Clay, pers. comm.).** (g) When asked about bonobos' interaction with water at Lola ya Bonobo Sanctuary, Democratic Republic of the Congo, Vanessa Woods said that bonobos at this place show an intensive interaction with water, especially certain individuals. She wrote about a fact that might be relevant for this unusual intensity of water use in this sanctuary: "They do get baths when they are infants in the nursery, up until they are moved into the larger enclosure at around five years of age; we have a large lake at Lola and many of the bonobos enjoy taking a dip" (Vanessa Woods, pers. comm.).

Common chimpanzees (*Pan troglodytes*)

(a) Nishida reported play behaviour at the water by a young wild female at the Mahale Mountains National Park in western Tanzania: "A young female, Tula, stood on all four near a pool in a running stream, and tried to bail the water out with one hand. Then she immersed herself in the water, splashed it and tried to uproot a submerged old buttress of a tree. She picked a large stone from the pool, carried it with both hands to a bigger, deeper pool and threw it into the water" (Nishida 1993, 25). **(b) Juveniles of M-group of the Mahale National Park, Tanzania, "stir water vigorously with one hand in a pool of a river. Juveniles do this when playing by themselves" (Nishida *et al.* 1999, 174).** (c) At Mahale, Tanzania, wild adult male chimpanzees were observed throwing stones into the river, which seemed to have a "great intimidating effect on other chimpanzees" (Nishida 1993, 25). **(d) Jane Goodall reported that water play is quite common among wild young chimpanzees. They were observed poking the surface with twigs, throwing stones into it, slapping it, and staring at it (Goodall 1995).** (e) Jill Pruetz observed wild juveniles playing intensively in water at Fongoli, in Senegal (Pruetz in Rubin et al. 2011). She wrote: "Adults as well as immature chimpanzees play in the water, although adults mainly soak during the beginning of

the rainy season when pools fill but when the temperatures have not yet fallen. Soaking and playing in water is typical of all chimpanzees in the community, although infants are somewhat uncertain around water when they are less than 1-2 years of age" (Jill Pruetz, pers. comm.). **(f) Vernon Reynolds reported on play behaviour by wild chimpanzees in the Budongo Forest in Uganda:**

> A proper account of play is not included here, but a single recent example is worth recounting, in which the play, rather unusually, involved water: On 8th February 2004 during a focal follow of Janie, her daughter Janet (aged almost four and a half years) was seen leaf sponging in the river Sonso. Five minutes later she was observed splashing with one hand in the water, from the bank of the river. Janie crossed the river on a pole bridge and Janet followed, but stopped on the bridge. Nora (a late stage juvenile aged eight years) joined her on the bridge and they both put one hand in the water and splashed, moving the water towards one another. Nora then left to play with Beti (a female aged seven and a half years). Janet followed her briefly but returned to resume splashing in the river, this time leaning over and splashing vigorously with both hands. Janet returned to do this twice more before joining Nora and Beti playing in the trees. (Reynolds 2005, 114-115)

(g) Angus reported from the semi-free ranging chimpanzee colony at the Aeromedical Research Laboratory, Holloman Air Force Base in New Mexico, which included 150 animals. In 1967, a group of chimpanzees was kept on an island surrounded by a water moat. Only two juvenile female chimpanzees ('Laveeta' and 'Annie') entered the moat, showing regular wading, playing and splashing behaviour (Angus 1971). **(h) Sheila Siddle reports from the sanctuary Chimfunshi in Zambia: "In all our enclosures we have ponds for them to get their drinking water. They are about two feet deep in the middle and we see lots of chimps playing in the water. One will stand there and deliberately splash anyone who is close at hand. They love this game. They also manage to get hold of plastic cool drink bottles and they take them to the pond to refill them" (interview with Sheila Siddle). Sylvia Jones reported from the same sanctuary:**

> Once the chimps had all quietened down the fun and games began. 'Karla' was the first to climb into the water pond, at first she just sat near the edge letting her fingers run over the top of the water. Finding this to be good fun she then began to move her knees up and down causing waves in the pond. She then jumped out of the water rubbing her back on the grass as if to dry herself. Suddenly she jumped up and almost dived back into the water, jumping up and down once again. She then lay in the middle of the pond on her tummy opening her mouth

> wide letting the water run into her mouth. Like a child in a new pond she played happily with the water. The other chimps watched. 'Sims' was keen to play but not too keen to get wet so he gently climbed into the pond paddled around for a few minutes and climbed out. Near by the pond was a rain puddle which amused him more as he managed to splash 'Karla' from a distance. 'DeeDee' was the next to wander into the water she just stood near the edge keeping a keen eye on the other chimps as if to watch that no one pushed her. It did not take 'Alice' long before she could see the fun and games one could have in the water. Jumping in from a distance she began to chase and splash 'Karla'. Running for cover she jumped out the pond and stood by watching and waiting until 'Alice' was not looking. She pounced back into the pond giving 'Alice' bigger waves. These two chimps played for well over an hour in the pond, chasing each other ducking faces under the water. (Sylvia Jones, pers. comm.)[56]

(i) Roxane Chantereau reports on the young female 'Shasa' from the J.A.C.K. sanctuary in Lubumbashi, Democratic Republic of the Congo: "When it's very hot, I sometimes organize water games with a water hose and she is the one to come first (Roxane Chantereau, pers. comm.). **(j) On hot days, Victoria Horner occasionally uses water from a hose as enrichment with chimpanzees at the Yerkes National Primate Research Center in Atlanta, Georgia, USA. According to her, several chimpanzees "seem extremely interested in interacting with a stream of flowing cool water, even though they have free access to cold drinking water all day". She describes different playing behaviours: running through the stream, purposefully sitting in front of it, wetting the hair on their forearms arms and drinking it as it pours off their elbows. "When a hose is used to make an arc of water, some chimpanzees run back and forth under it chasing one another in what appears to be a game. Some will hang by their feet from the ceiling of an indoor area and drink upside down, which again appears to be a form of play. Some bring objects such as buckets to the hose and fill them with water and float toys or food on the water, moving them around on the surface. There are, however, some chimpanzees who seem completely disinterested in water and show no interest in interacting with it" (Victoria Horner, pers. comm.).** (k) The fact that chimpanzees react in different ways towards water was described by Yerkes and Yerkes: "There is, according to our own observation, marked difference in degree of interest in water as a play medium. Of four animals which for many months have been under continuous observation in the Yale Primate

[56] The same text was used for a Newsletter from December 2008 from the sanctuary Chimfunshi published online in http://thezambian.com/2009/01/14/december-2008-newsletter/, assessed on 16 January 2014.

Laboratory, one, a male, eagerly avails himself of every opportunity to play in a bucket or tub of water. The others, if they do not entirely ignore such opportunity, seem to obtain less satisfaction from it. All of them dislike to have water thrown upon them" (Yerkes & Yerkes 1945, 216). **(l) Wolfgang Köhler described how young chimpanzees occupied themselves in various forms of continuous play, as for instance the young female 'Nueva': "Having once discovered that it was possible to dip up water out of the butt with her little drinking-cup, she incessantly dipped and filled the cup and then poured back the water into the butt. She hardly drank it at all, but even the drops that ran down the cup were of interest to her, and she loved to dip her hand into the water and watch the rain of drops fall from it" (Köhler 1959, 277); see also above "Washing food or objects".** (m) J. A. van Hooff, writing on the chimpanzee consortium at the Arnhem Zoo, The Netherlands, reports that suitable objects were used to "scoop up water from the moat, either in play or to drink". Sticks and twigs were used in various ways, e.g., "to 'fish' for floating objects in the ditch" (van Hooff 1973, 202). **(n) Crandall discusses the use of glass in zoos to protect visitors from chimpanzees throwing objects and spitting saliva or water at them (Crandall 1971, 144).** (o) The hand raised male 'Joe' liked to wade into the water at Chester Zoo, but only up to his hips. He liked to throw water at the visitors. (Mottershead 1960, 18-19). **(p) The young hand-raised male 'Cooper' plays regularly with soap bubbles in a tub (interview with Jill James), splashes regularly water with the hands or with the head during play, adopts different positions underwater (both in chest-deep water and hanging at a rope in 2 m deep water) and shows great variety of play with different objects and in interaction with humans (own observation with video footage).** (q) The young hand-raised female 'Christine' played at the edge of a pond, swished stick in the water, and used it to chase frogs (Hess 1954, 25). **(r) Ladygina-Kohts reported on two commonly raised human and chimpanzee youngsters:**

> The infants demonstrated many similar features during experimenting play with fire, water, and sand as well as with solid, elastic, transparent, or sharp objects. […] They were no less attracted to water. It is hard to name all of the pranks these little heads could think off when they saw water. Joni (the chimpanzee child) always took water in his mouth and made repetitive rinsing movements. Both did not miss the opportunity to splash water from a puddle. Sitting in front of a bowl of water, Roody (the human child), and Joni, scooped water with his hands or with a mug, poured it and scooped again. […] Both children were intrigued with tap water; they caught the running water with their mouths, stopped water with their

> fingers pressed to the faucet opening, and splashed cascades of water on themselves. (Ladygina-Kohts 2002, 361)

(s) Linda Brend, at the sanctuary Chimp Haven in Keithville, Louisiana, USA, said "we provide the chimpanzees with shallow pools in the summer and put fruit or bubbles in them for fun. They are happy to stick their arms into the water to pull the fruit out, but I have not seen any actually get into the water here. We do have a few that splash in the water in the pools with their hands" (Linda Brent, pers. comm.). **(t) Kris Hern, animal training manager at the Twycross Zoo near the village of Twycross in Leicestershire, England, wrote: "Samantha [...] plays with the water flow when filling up the bath and splashes it all around with one hand and also uses the waterfall in the outside enclosure to splash her face and it seems likes to wash her hands as she mainly does it after a scatter feed" (Kris Hern, pers. comm.).** (u) A press photo (author's collection) shows a chimpanzee during charging display (characterised by hair erection) directed towards an aquatic mammal. The chimpanzee is with one foot in the water and holding with one hand onto the vegetation on the shore of an island. It is close to what seems to be a sea-lion (Otariidae) with its head out of the water and apparently looking at the chimpanzee. The text attached to the photo was as follows:

> The Marquis of Bath's Longleat animal reserve gets more like the jungle every day. Now they even have gib [sic, big] game hunters! Simon, Alby and Mona, three tough old chimpanzees have lately taken to hunting the newly arrived Californian sea-lions. The three rough and ready old monkeys [sic] dangle their feet in the sea-lion's pool, enticing them to the edge – then they make a grab and try to catch them – for a snack! But luckily the sea-lions are too quick, and fortunately they don't usually take the bait. Simon gets right down into the water in the hope of persuading the sea-lion to come out – and be eaten – but fortunately the sea-lions are quicker than the chimps.

(v) The historic footage from a 1953 film depicting the juvenile chimpanzee 'Jerry' playing with water. 'Jerry' is filling a paddling pool with a hose. He sits in the pool, lies on his back and moves in the pool on his back. The commentator remarks that he shows this behaviour especially on hot days, and he does not like soap. 'Jerry' then saw a goose, took it by its neck and dragged it into the water. The goose tried to escape, but 'Jerry' continued to push the bird ruthlessly into the water; he tried once to submerge the goose, pushing on its back with both hands. After the goose escaped, 'Jerry' started

to play with a swimming pool shower, making the water rinse into his mouth (Universal International (producer) 1953). (w) A video showed a chimpanzee in a zoo using a stick to try to retrieve an object in the water moat (Anonymous 2009c)**. (x) A chimpanzee in a zoo saw a bird struggling in the water moat. The moat was limited by a glass wall on one side. The chimpanzee climbed along the wall and tried to take the bird with one hand, but the bird fell back into the water. The chimpanzee climbed back on land. Another chimpanzee approached the bird from the other side of the moat, but did not try to take it (Anonymous 2009d). (**y) Several chimpanzees at the Barcelona Zoo, Spain, were filmed begging for food by splashing water at the visitors and holding their hands in the air, some clapping their hands. They were separated from the visitors by a water moat with gentle slope. One individual was crouching on a concrete pipe in the water with the feet in water, another one stood up bipedally with the feed in water. The crouching individual reached out into the water to retrieve an object, went to another place at the shore and drank water, using his hand. Then he splashed water to the first individual still being in shallow water. The splashed individual went on land. The second individual went back on the pipe in the shallow water, stood upright for begging and crouched down, putting his mouth into the water (Anonymous 2011b).

5. Experiments and accidents in water

Drowning (or newspapers sometimes dubbing accidents as "suicide")

Gibbons (Hylobatidae)

(a) A young white-handed gibbon (*Hylobates lar*) in a zoo missed his grip on a branch and fell into water not more than 2 ft deep, and 3 or 4 ft from the island. "While it floundered helplessly, its mother watched from the shore but made no effort to assist it" (Crandall 1971, 129). **(b) A "gibbon in the London Zoo drowned even in very shallow water at the bottom of its large cage" (Schultz 1969, 45).** (c) Bev Carter explained that the Toronto Zoo has a moated area at the front of both the white-handed gibbon (*Hylobates lar*) and Sumatran orangutan (*Pongo abelii*) displays, so that bars, mesh or glass are not required to keep the animals in. "Years ago a baby gibbon did climb on the back of the Malayan tapir who shared the exhibit. The tapir did go into the moat which is shallowly shelved and is about 4 ft [1,20 m] at the deepest end; the baby may have fallen off or was submerged as the tapir accessed

the deep section and was unable to get back to the land. He unfortunately was found drowned" (Bev Carter, pers. comm.).

Orangutans (*Pongo pygmaeus*)

(a) According to zoo veterinarian and mammal curator Michael Flügger in the Hagenbeck Zoo, Hamburg, zoo visitors observed how the 10-year-old female 'Leila' tried to get a bread roll that had been lobbed into her enclosure by a visitor. She stood in rather deep water and held herself at a rope placed under water. Because the bread moved too far from her, she aimed to return to the shore. Suddenly she fell back, went down immediately and drowned in 1 m deep water. At the water surface only faeces and air were observed (Michael Flügger, pers. comm.). **(b) A juvenile orangutan in Lok Kawi Wildlife Park at Kota Kinabalu, Malaysia, fell in the water moat on April, 3rd, 2007 (the park was officially opened to the public on February 17, 2007). The accident was not observed, but a zoo visitor heard the sound of water splashing and alerted the zoo staff. He filmed two zoo-keepers pulling the dead animal out of the water (Anonymous 2007b).** (c) The Toronto Zoo has a moated area at the front of the Sumatran orangutan display. A juvenile male died as a result of being chased into the moat by a more dominant juvenile who was trying to take a biscuit (thrown by a member of the public) away from him. "He ran into the moat and unfortunately moved to the deep water rather than the shore. He was rescued and given mouth to mouth and CPR to resuscitate him. A team from the local children's hospital came up with the appropriate equipment to ventilate his lungs and he lived for 3 days before dying of pneumonia" (Bev Carter, pers. comm.). **(d) A sub-adult male at the Lion Country Safari Park in West Palm Beach, USA, drowned on August 31, 1973. He was placed on the island in August 17, 1972. The animal ran into the water in an attempt to retrieve a kidnapped infant from a female on the same island (R.B. Swenson, pers. comm. to Cousins 1978).** (e) A juvenile female at the Yerkes Field Station drowned on August 10, 1976. She was placed on the island in July 13, 1976. The accident was not observed (R.B. Swenson, pers. comm. to Cousins 1978).

Gorillas (*Gorilla gorilla*)

(a) At the Hannover Zoo in May 2000 the 16-year-old male lowland gorilla 'Artis' tried,, with the help of a stick, to get a leek that had been thrown into the moat of his enclosure by a visitor. He fell over a safety fence headlong into the 3.7 m deep moat and drowned (Schröder

2000). **(b) At the Bronx Zoo on May 13, 1951, the adult male 'Makoko' slipped from the edge of the moat, fell in the water and drowned in 6 ft deep water. His hands and occipital crest broke the water surface only once; it seems that he did not try to stand up and he did not show any attempt to swim. He stood 5 to 10 minutes under water, and all efforts at resuscitation failed (Anonymous 1951; Crandall 1951; Crandall 1971, 165). Crandall criticised newspapers' versions, which dubbed the accident as "suicide" (Crandall 1951).** (c) The young male 'Pong' drowned when floodwaters submerged the Prague Zoo's gorilla pavilion (Dewar 2005). **(d) The western lowland male gorilla 'Ben' drowned in a 4 ft deep moat at the Jacksonville Zoo:**

> Ben took a small step backward to turn and leave, but lost his footing and slid feet-first on his stomach down a short slope into the water. Although the water at Ben's point of entry was shallow and sloped relatively gradually to approximately four feet, he was not able to pull himself out and/ or did not know how to get out. Within two minutes, keepers were able to bring the other apes inside in order to gain access to Ben in the water. When staff pulled him out of the moat, Ben was non-responsive with no detectible pulse or respiration. (Williams 2007, 42)

(e) Adult female 'Anka' belonging to the Yerkes Primate Research Center drowned on May 30, 1973, at the Lion Country Safari Park. 'Anka' had been placed on an island with two other gorillas that had previously been placed there. She ran around briefly and then jumped into the water and drowned.[57] **(f) "The C.N.R.S. [Le Centre national de la recherche scientifique] had a small group of chimps and gorillas that were put on an island in the Ivindo River in [Makokou] Gabon that tried to leave during a dry spell, and most of them drowned" (Jack W. Bradbury, pers. comm.).** (g) Constanze Melicharek from the zoo Apenheul Primate Park in Apeldoorn, The Netherlands, wrote: "We have not had drowned

[57] I lost the original source referring specifically to the name ‚Anka', but I found the same episode reported in a newspaper:

> Two rare gorillas and an even rarer orangutan have died mysteriously at the famous Lion Country Safari zoo outside Atlanta. The animals were on loan from the respected Yerkes Primate center of Emory University which had hoped they would reproduce on islands at the zoo. But a male orangutan panicked while a female was being shot with a tranquilizer for medical purposes and jumped off a low cliff into deep water. A gorilla also leaped into deep water and a second gorilla apparently died of food poisoning.

Jack Anderson in *Time Daily* from 22 November 1973, p. 6, in: http://news.google.com/newspapers?nid=1842&dat=19731122&id=w_0rAAAAIBAJ&sjid=r8YEAAAAIBAJ&pg=3208,3885422; assessed on 16 January 2014.

apes or nearly drowned apes in the history of Apenheul, mainly thanks to the construction of the ditches" (Constanze Melicharek, pers. comm.).

Common chimpanzees (*Pan troglodytes*)

(a) 'Franzl', a 22-year-old male and head of the chimpanzees in the Münchener Tierpark Hellabrunn, Germany, died on 16 October, 2007. According to a spokesperson he took a running leap over the electric fence that separates the enclosure from the ditch, and died in the water (distanced covered in the air: 6,80 m). It is not known why he jumped over the fence. An autopsy showed that the animal did not have water in the lungs but had a haematoma the size of 30cm on the thorax. It is not clear why the chimpanzee died (Becker 2010). **(b) The 19-year-old female 'Püppi' in the Muenchener Tierpark Hellabrunn, Germany, died on 25 July, 2012, after she climbed over the fence, fell in the 2,5 m deep moat and drowned. Without witnesses, it is not known why she climbed over the fence, since she was calm and at the moment alone in the outdoor enclosure. It is possible that a visitor attracted her with food (Warta 2012).** (c) The 6-year-old male 'Dolisie' was released into the Tringle site at Conkouati Reserve, Congo, in November 1997. He fled immediately after release; his skeleton was located a week later 3 km from the release site. The cause of death was probably drowning or predation (Tutin *et al.* 2001, 1255). "It probably fell in the river during crossing or escaping from chimp attack/display" (Yann Le Hellaye, pers. comm.). **(d) The female 'Dimonika' (born in March, 1993) was released at Counkouati Reserve, Republic of the Congo, in July 2001; she drowned in March 2003 when she attempted to cross a river using overhanging branches, which broke (Goossens *et al.* 2005).** (e) From April of 1966 to August of 1967, five chimpanzees drowned in a moat at the Holloman Air Force Base, New Mexico (Angus 1971). **(f) Otto Adang wrote about the adult male 'Nikkie' at the Arnhem Zoo, The Netherlands. Nikkie was apparently eager to mate with a sexually attractive female. When he was allowed to go outside, he immediately ran at full speed and crossed the full length of the island (about 100 m). When he arrived at the moat, he jumped and did not make it to the other side. "Hij zonk als een baksteen" (He sank like a brick) (Adang 1999, 172). When he was pulled out of the moat a few minutes later, he was dead. Adang criticised a newspaper version, which dubbed it a "suicide" (Adang 1999, 172-173).** (g) In the Antwerp Zoo in Antwerp, Belgium, one individual "drowned quickly in the moat of the new ape-house" (Schultz 1969, 45). **(h) At the Dublin Zoo, the 17-year-old female 'Annie' tried to escape from a male and entered the water with her two-**

year-old male infant 'Angus' on her back. The moat did not have a gradual slope, so both went down and died. When the bodies were recovered, the infant was still holding the mother. The female was stressed by the other chimpanzees after she was introduced recently to this group (Gerry Creighton, pers. comm.) (see Anonymous 2000 for an unconfirmed, slightly distorted version). (i) An adult male at the Lion Country Safari Park in West Palm Beach, USA, drowned on May 25, 1973. He was placed on the island on July 17, 1972. The animal was anaesthetised for medical reasons on the day before the accident. The drowning was not observed (R.B. Swenson, pers. comm. to Cousins 1978). **(j) One adult female at the Yerkes Field Station drowned on May 23, 1977. She was placed on the island on April 20, 1977. This animal was found dead in the water with extensive bite wounds. She had probably been driven into the water by an adult male in the group (R.B. Swenson, pers. comm. to Cousins 1978).** (k) One adult male at the Johannesburg Zoo, South Africa, drowned in the 1990s after trying to climb a wall and falling into a 3 m deep moat (interview with Katherine Visser). **(l) The 8-year-old male 'Amber' at the Johannesburg Zoo, South Africa, tried in 2009 to escape from two other males jumping over the electric fence into the 2-3 m deep moat. Zoo keeper Armstrong Mdoda saw how 'Amber' stood upright on the bottom of the moat, only the waving hands showing out of the water. He did not make any attempt to swim. Mdoda ran to switch off the electric fence placed between the exhibit and the moat. When he came back, another zoo-keeper was already in the moat, trying to pull out 'Amber'; unfortunately it was too late (interview with Armstrong Mdoda).** (m) Fouts reported on the drowning of 'Candy': "But Washoe couldn't protect Candy twenty-four hours a day. One morning I couldn't find Candy and I became worried that she had attempted to jump the moat and had drowned. My students and I waded into the water up to our chest and began dredging the muddy bottom with poles. After an hour or so, I felt her small body under my feet, and went down to retrieve it" (Fouts 1997, 179). **(n) In 2003, Gamble et al., requested complete gross and histopathology reports from the holding institutions by the Chimpanzee Species Survival Plan (SSP)® Veterinary Advisor (Gamble *et al.* 2004). According to this review, in the period between 1990 and 2003, 94 chimpanzees died in zoos that are currently accredited by the American Zoo and Aquarium Association. They wrote: "Exhibit related mortalities included drowning (n = 7), post-escape recovery efforts (n = 3), and entrapment in an exhibit prop (n = 1), or 12% of the total deaths, with an average age of 15.2 yr of age (range = 15 mo to 37 yr)" (Gamble *et al.* 2004, 562). Owing to the fact that the**

predominant cause in this category was drowning, this study supported the current Chimpanzee SSP® recommendation against water moats as primary containment (Gamble *et al.* 2004). (o) Before the erection of a barrier in a moat at the Antwerp Zoo, a chimpanzee was drowned by falling headlong into the moat (van den Berg, quoted in Cousins 1978).

Experiments showing lack of swimming ability

Gibbons (Hylobatidae)

(a) In an attempt to refute the hypothesis that gibbons use the air sac as a swimming bladder (see chapter 3.4.1), a siamang (*Hylobates syndactylus*) was placed a large tub of water: "[H]e was much frightened at his situation, and soon began to display a marked hydrophobic symptom, but not the least attempt was made to inflate the pouch, although he was frequently submersed" (Bennett 1834, 152). **(b) The primatologist Clarence R. Carpenter describes an experiment with a gibbon:**

> Gibbons may be said to be superbly arboreal, inadequately terrestrial and almost helpless in water. On May 18, 1937 a fully adult female gibbon was repeatedly tested for swimming ability in a calm pool of water near my camp at Doi Dao. Taking the ape by the hand, I gently threw her about six feet from the bank into water several feet deep. The responses of the animal consisted of throwing back and raising its head, general struggling movements, threshing about and uncoordinated movements of legs and arms. The thick long wool rapidly became water soaked and in less than a minute, on three successive trials, she began to sink. I pulled her ashore with the light cord which was tied around her hips. (Carpenter 1941, 78-79)

(c) A similar experiment was described by Geo Candler:

> There is a point about the Hoolock that strikes me as very extraordinary, and that is the fact that he cannot swim. I had been told this by both natives and Europeans, but I confess I was somewhat sceptical about it until I tried experiments myself. We put a full-grown Hoolock into a big tank in 10 feet of water. He struggled helplessly, as a boy would before he learns to swim. He sank twice, with head thrown back and arms waving frantically, and we were obliged to rescue him almost asphyxiated and choking in the most human way.(Candler 1903, 188)

Near drowning and rescues by a human after falling or entering in water

Orangutans (*Pongo pygmaeus*)

(a) A near drowning occurred in the autumn of 1950 in the uncompleted new orangutan building at the Bronx Zoo. The approximately 4-year-old female ‘Sandra’ was placed in the outdoor yard to test her reaction to the moat; a keeper was to observe her until the experiment had been completed, but an emergency called him away for few minutes. On his return, a slight rippling of the surface of the moat suggested that ‘Sandra’ was drowning. Leaping into 3 ft. of water, the keeper quickly found her weakly fumbling about on the bottom, making no proper effort to come out of the water. First-aid treatment brought complete recovery (Crandall 1971, 136). **(b) The 9-year-old male ‘Pagy’ in the Prague Zoo, in an attempt to climb and swing upon some palm foliage, fell into the deepest part of the water moat; a keeper jumped into the water and rescued him (Dickinson 2010).**

Gorillas (*Gorilla gorilla*)

(a) The western lowland male gorilla ‘Quito’ fell or went to a moat at the Jacksonville Zoo on June 30th, 2005. When he managed to pull himself out of the water he was on the “wrong side”, in the chimp enclosure. Once on land, ‘Quito’ was attacked by all three chimpanzees. “We are not sure how Quito initially got into the moat, but guests and staff observed Quito's struggle in the water and reported that he went completely under several times” (Williams 2006). **(b) Male gorilla ‘Robbie’ at the Arnhem Zoo, The Netherlands, “jumped into his moat after only an hour of first access to his outdoor enclosure. Fortunately he was being watched and was safely landed with a long pole. After this experience neither he nor any of the other apes, who must have been watching, ever approached the water again" (Van Hoof, pers. comm. to Cousins 1978, 8-9).** (c) Van den Berg reported that, on two occasions, two young gorillas in the Antwerp Zoo fell into their moat. The wire between the shallow and deep part of the moat prevented them from drowning. On both occasions they were able to climb out of the water by themselves (van den Berg, quoted in Cousins 1978).

Common chimpanzees (*Pan troglodytes*)

(a) Chester Zoo has kept apes on islands since 1956. In 1957, a baby accidentally fell into a water moat. The mother ‘Meg’, sitting on a tree nearby, jumped off to rescue her baby by grabbing it. However, both animals then landed in the moat. She scrambled out on the wrong

side of the moat, and the zoo staff was not able to persuade her with planks or ladders to cross back. A window was removed from the indoor quarters to allow her to carry her baby back. This was the first occasion that a chimpanzee had crossed the moat (Mottershead 1960, 19). **(b) From April of 1966 to August of 1967 four chimpanzees were rescued by Air Force or UCLA personnel at the Holloman Air Force Base, New Mexico. They either pulled them out with a pole or waded into the moat to take them out of the water. In some cases the animals fell into the water accidentally, in other cases they jumped into the water to escape from another chimpanzee. In all cases the animals appeared to be in a state of panic; they splashed furiously and sank quickly, without showing any signs of swimming movements. The major safety device for the animals was a chain link fence which has been attached to the bank on the island side of the moat, nearly reaching the moat bottom (Angus 1971).** (c) Otto Adang reported on a juvenile that he rescued from drowning: "Fons (the juvenile I saved) […] jumped into the moat during a conflict to evade his attackers, but only got half way (in his case also I think he tried to cross the moat)" (Otto Adang, pers. comm.). **(d) In 1990, the adult male 'Jojo' fled into the moat after being attacked by another adult male in the Detroit Zoo, USA. Zoo visitors, Rick Swope and his family, "watched the chimpanzees for probably about half an hour or so and we were just getting ready to go when I heard a splash. I just caught out of the corner of my eye this chimpanzee flying through the air" (Swope in Anonymous 1990, 30). "Everyone in the whole place was just standing around watching this monkey [*sic*] drown. When he went down the second time I knew I had to do something" (Swope in Anonymous 1990, 30). He scaled the fence, plunged into the water and "managed to grab the chimp on his first try, but it slipped from his grasp and sank to the bottom" (Donovan 1990, 3). Rick Swope said: "The water was so dirty, I couldn't see through it. I swam around on the bottom until I found it. Then I pulled it up. I could see it was still alive. It was looking at me. I think it knew what was going on. It never made any attempt to do anything to me"(Swope in Donovan 1990, 3); the scene was captured on video (Anonymous 2008b); see also discussion on exhibit designs (chapter 4.3.6).** (e) Kortlandt reported on two individuals that had great difficulty in coming out of the water: "I have myself observed two cases in which chimpanzees would have drowned in a 5 ft-deep moat if they had not been rescued by an attending scientist. Their behaviour underwater was striking and dramatic: instead of simply trying to walk quadrupedally to the nearby shore, they stood upright and made little jumps while alternately extending one or the other hand helplessly into the air

(Kortlandt 1975, 648). **(f) Anna M. Noell took the young male 'Kongo' on her back to the beach and waded about waist-deep. The animal panicked, tried to jump back to shore and fell in the water, where he remained completely immobile. He sank to the bottom, without showing any effort to swim (Noell 1979, 144).** (g) Reynolds reports on rescues of drowning chimpanzees: "I have myself on two occasions helped to pull chimpanzees out of a water-filled moat in which they were quite clearly drowning, and I am convinced they cannot swim, although in their struggles as they flounder about they can sometimes make a little headway in the water" (Reynolds 1967, 188).

Drowning individuals rescued by apes

Orangutans (*Pongo pygmaeus*)

A visitor to US zoo captured an orangutan on video 'saving' a nestling bird struggling in a moat. Following report published in *The Telegraph* describes the video:

> It yanked a leaf from a nearby bush and extended its arm out to the bird, beckoning to the chick in the hope that it will latch onto the leaf. Onlookers cheered as orangutan managed to get the bird to grip the leaf for a split second only to have the bird drop again. In a last-ditch attempt to rescue the chick, the orangutan gently waved the leaf in front of the bird which managed to latch on to it. The ape plucked the bird from the water to the delight of the crowd. (Anonymous 2011e)

Gorillas (*Gorilla gorilla*)

Cousins, referring to a letter published in the *Sunday Express* (UK) in September 19, 1976, wrote about a swimming mouse which was "rescued" by a gorilla at Chester Zoo:

> It struggled to the sloping side of the pool and hung on precariously. A gorilla approached the tiny rodent, crouched near it, and put out a finger to gently propel the mouse an inch or so up the slope. The ape then turned away but the mouse was very weak and tried to climb further up the slope. The gorilla crouched beside the mouse, and this time it put out a finger and thumb and gently lifted the minute creature in the air and put it safely on the cage floor. The human spectators of this touching display applauded and cheered the gorilla. (Cousins 1978, 9)

Common chimpanzees (*Pan troglodytes*)

(a) Jane Goodall reported on an adult male chimpanzee who drowned as he tried to rescue a chimpanzee infant who fell in water (Goodall 1990, 213). **(b) Anna Mae Noell wrote a book entitled *The History of Noell's Ark Gorilla Show* (Noell 1979), an account of a small family-type show that toured during decades the eastern seaboard states in the USA. A special attraction of the show depended on people of the audiences, who, inside of a cage, boxed, wrestled or foot-raced with adult chimpanzees. These chimpanzees were raised by Anna M. Noell and her family. The book contains detailed and - as far as can be judged (see chapter 4.1.1) - credible reports on the interaction between apes and humans. Anna M. Noell wrote about a situation in which male 'Snookie' helped the six-year-old human owner's son Bob:**

> Snookie had what seemed to us an unreasonable fear of water, which caused Bob a great deal of amusement, because the little fellow would scream in terror every time Bob walked towards the water. Along the edge of the levee at that particular spot, there was a retaining wall of black tar, which was sloped at such an acute angle as to be impossible to stand upon. Somehow Bobby had walked unnoticed to the brink of the wall and lost his footing. Too terrified to scream, he held his weight out of the water by a mere clump of grass. Snookie saw Bobby's plight and ran to the water's edge and pulled the child in by offering Bobby his foot, almost before Bob could grasp why Snookie had suddenly abandoned his fear of the drink. I feel not as I felt then - if Snookie hadn't done just what he did, we probably would have had no little boy, next day. Bobby was only six years old at the time. After this experience it was harder than ever to get Snookie up on that levee! (Noell 1979, 21)

(c) Roger Fouts reported on a new female, named 'Penny', who was introduced to a colony of chimpanzees, kept on an island. In the same afternoon, while playing by the shoreline, Fouts suddenly heard Penny screaming in terror from the other side of the island. Fouts assumes that she must have panicked at being left alone with the other chimps. The next thing he heard was "a loud splash, the sound of Penny hitting the water in the moat". He continued:

> She had taken a running start and vaulted over the electric fence. As I neared the fence I was surprised to see Washoe sprint ahead of me and leap over the two electric wires. She landed, thank heaven, on the narrow dirt ledge that dropped sharply off into the pond. After sinking like a stone, Penny had now surfaced near the island's shore and was thrashing about wildly. Then she submerged again. With one hand grasping the bottom of an electric fence post,

> Washoe stepped out onto the slippery mud at the water's edge. She reached out her other long arm, grabbed one of Penny's flailing arms, and pulled her to the safety of the bank. (Fouts 1997, 179)

Possible suicide

Common chimpanzees (*Pan troglodytes*)

At the Lion Country Safari Zoo in West Palm Beach, USA, a male jumped from a bridge into the water moat without clear, immediate reasons and in front of several zoo visitors. He drowned without visible struggle. He had experienced severe stress in the time before with the other chimpanzees. This incident was judged as possible suicide by the director of the zoo Terry Wolf (interview with Terry Wolf).

Use of water in attempts to drown conspecifics / individuals being pushed into water by conspecifics /use of water to avoid aggressive conspecifics

Orangutans (*Pongo pygmaeus*)

The ex-captive female infant ‘Doe’, a rehabilitant in the Tanjung Putting Reserve in Borneo, was probably drowned by the 7-year-old male ‘Sugito’. A few months earlier, the body of a female infant was found drowned and mutilated. “It was unmistakably the work of an orangutan. Shortly afterwards, Sugito had caught another female infant and held her face down in the river until we rescued her” (Galdikas 1980, 832). Biruté Galdikas reported that Sugito also drowned a kitten (Galdikas 1998, 525).

Bonobos (*Pan paniscus*)

Zanna Clay reported on bonobos observed at Lola ya Bonobo Sanctuary, Democratic Republic of the Congo. She noted that entering rather deep water is also used to avoid an aggressive individual: “One male stands in the lake to avoid aggression as the females are less courageous to go to the deeper areas, so he can make a quick escape. Males generally are braver and spend much more time in water than the females” (Zanna Clay, pers. comm.).

Common chimpanzees (*Pan troglodytes*)

(a) Two adult females kidnapped an infant and drowned it in the water moat at the Lion Country Safari Park in West Palm Beach, USA; they brought the dead baby back to its mother (interview with Terry Wolf). **(b) Angus reported from the semi-free ranging chimpanzee**

colony of 150 animals at the Aeormedical Research Laboratory, Holloman Air Force Base in New Mexico. In 1967, a group of chimpanzees was kept on an island surrounded by a water moat. Only two juvenile female chimpanzees ('Laveeta' and 'Annie') entered the moat, regularly showing wading, playing and splashing behaviour. They also entered the moat to escape from dominant animals. The dominant male 'Tim' pushed 'Annie' repeatedly into the moat, and she did not drown only because of her aquatic habituation. In fact, she waited in waist-deep water until 'Tim' left the shore (Angus 1971). (c) One-year-old chimpanzee 'Vendii' at the Tulsa Zoo, USA, was filmed walking toward the water moat, followed by another juvenile. As soon as 'Vendii' sat close to the moat, looking to the water, she was pushed by the other chimp and fell into the water. 'Vendii' fell in shallow water, screamed and immediately tried to climb out. Three adult chimpanzees immediately rushed to her, and one (probably the mother) pulled her out 1.7 seconds after 'Vendii' had fallen into the water (Anonymous 2008d)

Feeding in or at water bodies

Orangutans (*Pongo pygmaeus*)

(a) Russon reported on rehabilitant orangutans in Indonesia taking and eating fish from the water (mostly dead fish floating, but some alive) (Russon *et al.* 2010b, 291). **(b) Schuster et al., reporting on the same population of orangutans of the rehabilitation centre in Indonesia, wrote: "An orangutan has made a "fishing-rod" and is fishing floating fruit out of the River Rungan" (Schuster *et al.* 2008, 96); six photographs illustrate the behaviour.** (c) One orangutan from the BOS island of Kaja made repeated attempts at „spearfishing in the Gohong River, as he had seen the native men do. He did not succeed with his clumsy tool, and therefore changed tactics and used his stick to pull the laid-out-fishing lines from the water [...], thus stealing the hooked prey" (Schuster *et al.* 2008, 98); three photographs illustrate these behaviours. **(d) Schuster et al. wrote: "After several failed attempts an orangutan beats a fish that was swimming past with a baton and eats the prey" (Schuster *et al.* 2008, 110); three photographs illustrate the event.** (e) Schuster et al. wrote in the legend of a photo from an orangutan hanging on branches and taking something from the water surface: "Dexterity and long arms pay off for one of the inhabitants of the rehabilitation island, Kaja, in the province of Central Kalimantan, Borneo. He is fishing fruits out of the Gohong [River]" (Schuster *et al.* 2008, 120).

Gorillas (*Gorilla gorilla*)

(a) In and around the northern part of the Odzala-Koukoua National Park in the Republic of the Congo there are more than 100 forest clearings, known as "bais". Gorillas visit these clearings on a regular basis to feed on aquatic plants. Swamp forests are considered important habitats and feeding areas for western gorillas, supporting them in high densities both in the wet and the dry season (Fay 1989). **(b) At the same site another study showed that feeding activities occupied 72% of the time that visiting gorillas spent on the clearing. They fed on four plant species which have higher mineral contents (especially Na and Ca) than the dominant species that constituted the main food for gorillas in this forest. The four preferred swamp plants also have a higher potassium content and contain less lignin than non-eaten clearing plant species. These results suggest that the mineral content (especially in Na, Ca, and/or K) could determine the feeding selectivity of gorillas at the clearing (Magliocca & Gautier-Hion 2002).** (c) Western lowland gorillas in the Lopé reserve in central Gabon were seen in marshes and streams, where they feed on three species of semi-aquatic plants: *Marantochloa cordifolia*, *M. purpurea*, and *Halopegia azurea*. These plants are typically about 1 m high and occur in streams and marshes. "They move down the middle of streams, in water about 30 cm deep, uprooting plants from both banks." From May 1984 to April 1985,there were 64 occurrences of this behaviour recorded, and all seven known groups in this area were involved in this behaviour (Williamson *et al.* 1988). **(d) Kuroda and colleagues reported on a study on sympatric chimpanzees and western lowland gorillas in the Ndoki Forest, Congo. The main study site covered a tropical forest of about 20 km, and is located in the southwest of Nouabalé-Ndoki National Park, Congo. There are clearings with aquatic herbs along the watersides in the swamp forest. "Thus, swamp vegetation, occupying 15-20% of the study area, is used almost exclusively by gorillas" (Kuroda *et al.* 1998, 76).** (e) Another report from the same site confirms that gorillas frequently foraged on swamp vegetation. Most swamp observations of gorillas were made when they were feeding on *Hydrocharis* and this occurred regularly through the seasons (Nishihara 1995). **(f) One study reported that western lowland gorillas used swamps as feeding grounds frequently (27% of the days) and incurred a 50% increase in daily path length compared to mountain gorillas. The 77% variation in monthly frequency of swamp use was explained by ripe fruit availability within the**

swamp, and not by the absence of resources outside the swamp (Doran-Sheehy *et al.* 2004).

Bonobos (*Pan paniscus*)

(a) In the large shallow swamp of the eastern Congo Basin several wild individuals showed no reluctance to feed on aquatic plants in shoulder-deep water. This behaviour was observed for at least two consecutive months (Uehara 1976). **(b) Several wild individuals were observed eating shrimps in shallow water (Barbara Fruth, pers. commun. reported in De Waal & Lanting 1997, 80).** (c) Badrian and Malenky (1984) observed wild individuals eating aquatic or semi aquatic plants. Furthermore, the rapid movements by some individuals in water "suggested that they were feeding on small animals (fish or shrimp) that are abundant in the shallows" (Badrian & Malenky 1984, 291). **(d) In the swamp forest in Wamba, DRC, wild bonobos forage for earthworms more persistently than in the forest of the *Gilbertiodendron* primary forest. When searching for earthworms in the swamp forest, the bonobos did not dig clearly defined holes as they did in the primary forest. Rather, they moved slowly in the shallow stream or adjoining mud beds, pushing the mud aside with their fingers. One group spent almost three hours in a small stream foraging for earth-worms. However, the consumption rate for earthworms was very low, ten times lower than the foraging rate in the forest (Kano & Mulavwa 1984, 258-259).** (e) Wild bonobos of the eastern Congo Basin were observed feeding on aquatic plants for at least two consecutive months. In doing so, they immersed themselves in water up to the shoulder (Nishida 1980, 194-195). **(f) Observations of bonobos at the perennial pools of the Lukuru Wildlife Research Project (DRC) confirm that bonobos are not afraid to enter waist-deep water. Chimpanzees at Bossou had invented a tool to 'sweep' for algae similar to algae eaten by bonobos at the Bososandjia pools of Lukuru. Using their tool, the chimpanzees gathered the algae from the shore, avoiding the water, while the bonobos of Lukuru waded waist-deep into the pools to gather algae and subaquatic vegetation. For the bonobos, inventing a specialised tool for aquatic food acquisition was therefore unnecessary. (Myers Thompson 2002, 66).** (g) Wild bonobos at Lilungu (Ikela), Democratic Republic of the Congo, were observed washing food (e.g., earth-worms, aquatic plants, or muddy roots) before eating. They were observed digging earth-worms in the beds of streams in the swamp forest (Bermejo *et al.* 1994). **(h) Randall Susman collected data on wild bonobos in Equateur, Democratic Republic of the Congo, wading in water and**

recovering the remains of fish and crustaceans in their faeces (Susman et al. 1980). He thinks that "bonobo collecting of fish is relatively rare and a small part of their diet. They also eat insects and small mammals more infrequently than they do fish" (Randall Susman, pers. comm.). (i) One adult individual was filmed in a sanctuary in the Democratic Republic of the Congo while eating aquatic plants (Woods 2009) (Vanessa Woods, pers. comm.). **(j) In the Lola ya Bonobo Sanctuary, Democratic Republic of the Congo, Zanna Clay observed a male "using a stick to balance in deep water, while fetching a floating fruit" (Zanna Clay, pers. comm.).**

Common chimpanzees (*Pan troglodytes*)

(a) The behaviour of wild chimpanzees of the Mahale Mountains, Tanzania, in relation to water has been described in detail (Nishida 1980). These chimpanzees are known to consume more than 200 species of plants, including at least two species of aquatic *Cyperus*. Chimpanzees of the M-group have been observed feeding on the pith of *Cyperus*, occasionally wetting their arms and legs in the swamp in the Kasoje Forest. This behaviour was not observed in the K-group, since there is not such a swamp within their range. Nishida reported a behaviour from an M-group chimpanzee in October 1965, i.e., before the habituation of this group. He once heard the chimpanzee walking in a rapidly running stream (2.5 m wide and 40 cm deep). After the chimpanzee fled, he found remnants of a freshly eaten *Myrianthus* fruit on a small rock in the center of the stream. "The chimpanzee surely waded the stream and ate the fruit on the rock on the way" (Nishida 1980, 195). **(b) In the same region, the wild female 'Sally' was repeatedly observed in 1997 entering a stream and repeatedly picking up algae with one hand and putting it into her mouth. She advanced slowly into water up to the knees and fed a large amount of algae (Sakamaki 1998).** (c) Wild individual chimpanzees of the Bossou community, Guinea, were observed using a stick to gather floating algae (*Spirogyra sp.*) from the surface of ponds, a behaviour which was later defined as "algae scooping". One chimpanzee was observed selecting a stick, breaking it off with his teeth and forming a fishing 'rod' free of leaves. The tool was inserted into the water and with a scooping action of the wrist the surface algae were fished out. The stick was then brought up to the mouth and the algae eaten (Matsuzawa & Yamakoshi 1996). **(d) Devos and colleagues reported:**

> [In a forest clearing at the Odzala National Park in the north west of the Republic of Congo] three male chimpanzees entered the clearing at 11.24 hr and quickly walked to a small flood pool. They were clearly identified by distinctive physical characteristics. One of them stood quadrupedally while the two others sat by the water. Two chimpanzees, using their fingers, removed the algae filaments from the pool and ate them by putting their fingers into their mouth. The third chimpanzee, who was sitting uprooted a whole (about 20 cm long) herbaceous plant, a sedge (Cyperaceae) and clipped off the head, using his incisors, leaving the stem. He held the stem between the third and the fourth digit and immersed it into the water, withdrew it, then cautiously put it to his mouth, the stem covered with green algae. When he walked from one pool to another, the chimpanzee carried the tool between his pursed lips. The three chimpanzees spent 71 min at the clearing, and most of this time was devoted to algae feeding. The same three individuals were later seen on 4 November (12:57–13:53 hr), and on 6 November (11:38–13:16hr), the tool-using male performing the same scooping behaviour while the two others still feeding using their hand. On 4 November, the tool-using chimpanzee left the clearing with a tool in his mouth. (Devos *et al.* 2002)

(e) Water was used as part of an enrichment programme at a sanctuary in Uganda. "In one game, peanuts were placed in a large barrel of water, just out of reach. The chimpanzees therefore had to use sticks to fish for them" (Victoria Horner, pers. comm.). **(f) J. A. van Hooff, writing on the chimpanzee consortium at the Arnhem Zoo, The Netherlands, reported how some animals occasionally succeeded in catching goldfish from the moat with their hands: "They were highly fascinated by the dying fish as it jumped about on dry land. Although the fishes were damaged and traces of biting were observed, they were never seen to be eaten" (van Hooff 1973, 202).** (g) Kris Hern, animal training manager at the Twycross Zoo near the village of Twycross in Leicestershire, England, observed: "The chimps in chimp complex and Rikis group do have access to a small bath area which can be filled with water. I have found that they are intrigued by the water and will fish out items if they are floating (especially food items)" (Kris Hern, pers. comm.).

Drinking behaviours

Gibbons (Hylobatidae)

(a) Gibbons often drink water from leaves or by putting their hands into water and then licking it up from there. They may also try to lap, but it takes them a long time to collect any water in this way (McCann 1933, 404). **(b) Carpenter reported on the drinking behaviour**

of wild gibbons in Thailand: "The sources of water for gibbons are, in the order of their importance: 1. Water content of fruit and leaves. 2. Surface films of water collected from rains and heavy dews on leaves, bark and on the animals' own coats. 3. Water collected in the hollows of tree trunks and large limbs. 4. Pools of water, streams and springs or even water seeping from crevices in rocks. Keen competition among groups occurs around limited sources of water such as seep bogs or springs during long dry seasons" (Carpenter 1964a, 196-197). (c) Van Gulik reported on the drinking behaviour of gibbons: "[T]he gibbon drinks by licking the dew or rain water sticking to leaves, or from water accumulated in tree hollows. The latter he drinks in the typical gibbon manner, namely by moistening the fur on the back of his hand, then sucking it. This method the gibbon retains in captivity, dipping his hand in the cup or saucer of fluid offered him. The gibbon comes down to the ground only in the dry season, when no water can be obtained up in the trees, and drinks from rivulets, lakes or other watering places" (Van Gulik 1967, 7). He therefore interprets a Chinese legend of gibbons forming a chain to drink as erroneous:

> [A] thousand years old Chinese tradition maintains that gibbons will never come down from their trees to the water's edge to drink, but reach the water by forming a chain, holding each other's hands and feet. But although I have often seen two or three gibbons hanging on each other in play, I have never seen them deliberately adopt this method for reaching from a high place an object down on the ground. The Chinese predilection for representing on their painting and in sculpture gibbons hanging in chain-formation must have been inspired by their love of quaint and artistic effects rather than by actual observation. (Van Gulik 1967, 7)

(d) Delacour described gibbons as disliking water, except for drinking: „[They] very generally do [this] by dipping their hand and sucking it, but they can also drink by putting their lips into the water. This is especially true of young ones" (Delacour 1933, 72). (e) Discussing the alleged behaviour of gibbon mothers washing their babies, Yerkes and Yerkes suggest that this impression comes from "the behavior of the female as with baby clinging to her breast she bends over to dip water from a pool and lick it from her hand. We can readily imagine that the female gibbon, observed at a distance, drinking in its peculiar fashion might appear to be washing its infant" (Yerkes & Yerkes 1945, 59). (f) Captive gibbons were described as to use leave sponges or cloth sponges to drink water (Shumaker *et al.* 2011, 109).

Orangutans (*Pongo pygmaeus*)

(a) Van Schaik described different drinking techniques used by wild orangutans in Indonesia: (a1) Drinking from pitcher plant's cup is common wherever pitcher plants are common and is therefore considered to be a universal (Van Schaik *et al.* 2006, 862). (a2) Drinking water from the ground using a leaf as vessel and drinking water using crumpled leaves like a sponge are both described as rare behaviours (Van Schaik *et al.* 2006, 860). (a3) Drinking from tree holes by inserting a leafy branch and collecting the water dripping from the branch is a behaviour present only in certain areas (Van Schaik *et al.* 2006, 853). **(b) In his investigation of play behaviour in animals, Brown described (showing a photo) an orangutan in Sumatra hanging upside down from a tree to drink and to play with the water (Brown 1994, 2).** (c) A similar photo of the rehabilitant female 'Sobiarso' hanging upside down and drinking in this position was shown by Galdikas. She reported that she also observed this behaviour by wild orangutans (Galdikas 1980, 848). **(d) Harrisson reported on an observation of drinking behaviour in a rehabilitant orangutan in the Bako National Park in Borneo: „Round about ten the three Orangs became active again. One climbed into a low tree nearby, where a large branch had broken off. He scraped around in a hollow which had filled up with water, bent right down with protruding lips to sip, then put his hand in the puddle and scooped out leaves and water. He inspected his hand and turned it round to suck more moisture from the wet hair on the back of his fingers" (Harrisson 1987, 79)**.

Gorillas (*Gorilla gorilla*)

(a) In the first half of the 20th century, little was known on about the drinking behaviour of wild gorillas. Hoyt reported that "yet the African natives in the gorilla country say that gorillas never drink any water from streams or pool but only the dew from the leaves. And it is true that in Africa we never found any gorilla tracks near a river bank" (Hoyt 1941, 119). (**b) Carpenter described the behaviour of the two mountain gorillas, 'Ngagi' and 'Mbongo' at the San Diego Zoological Park. He reported that these animals drunk large quantities of water daily. Normally they would bend over the water and drink with their lips in the water. But when excited, they would take the water with their hands, hold it over the head and let it run into their mouths. They also used small containers to take**

water and drink from them (Carpenter 1964b, 112). (c) In a documentary[58], a family of western lowland gorillas in the Democratic Republic of Congo was filmed when entering a forest stream. One silverback male and a female entered the very shallow water of the stream walking quadrupedally; the male began to drink directly from the stream (with the lips in the water). Another scene shows an adult gorilla walking quadrupedally in shallow water, dipping the left hand in the water and pouring water in the mouth to drink.

Bonobos (*Pan paniscus*)

(a) S. Kuroda reported to Kano that he only once observed wild bonobos drinking from standing water (Kano & Mulavwa 1984, 244). Kano noted that wild bonobos rarely drink from running or standing water (Kano 1998). It appears that they obtain practically all the water they require from their food (Kano & Mulavwa 1984, 244). **(b) According to Zanna Clay, bonobos at Lola ya Bonobo Sanctuary, Democratic Republic of the Congo, drink water from lakes, streams, they also fill their own plastic bottles from streams to drink with and play with (Zanna Clay, pers. comm.).** (c) In a sanctuary in the Democratic Republic of the Congo, one adult female bonobo carrying an infant was photographed standing bipedally in water up to her knees and bending down, taking water to her mouth with her hand. Probably the same female was filmed sitting at the water and pouring water to her mouth with one hand (Anonymous 2011g).

Common chimpanzees (*Pan troglodytes*)

(a) In 1963, Jane Goodall reported that „chimpanzees were never observed drinking, although on several occasions a single animal or a group were seen heading towards a stream, remaining out of sight for five to ten minutes and then returning the way it came. It seems likely that these animals were drinking. This behaviour was seen on four occasions between 11.00 and 11.30 a.m. and six times in the afternoon between 3.00 and 4.00 p.m.“ (Goodall 1963, 46). **(b) Some two years later, Goodall reported on an observation of drinking from a stream: „A chimpanzee was observed drinking only once: it went to the edge of a stream, put its face down, and sucked up water with its lips for about 30 seconds“ (Goodall 1965a, 446).** (c) Already earlier, Nissen reports twice observing wild chimpanzees

[58] ***Mythos Kongo – Im Reich der Menschenaffen*, director Thomas Behrend, production Blue Planet Film; aired at ORF on 14.01.2014. See also** http://tvthek.orf.at/program/Universum/35429/Universum-Mythos-Kongo-Im-Reich-der-Menschenaffen/7326072/Universum/7353604**, assessed on 16 January 2014.**

drinking: "Crouching at the bank of a tiny stream, hands and feet on solid ground, the ape lowered his head until his lips were in contact with the water. The water was apparently sucked, rather than lapped up" (Nissen 1931, 61). **(d) Reynolds and Reynolds noted that no similar observations were made at Budongo in Uganda, probably because of the difficulty of seeing anything on the ground. "However", they wrote, "drinking was observed on one occasion in a Maesopsis tree". They continued:**

> A fault in one of the branches at about 70 feet had led to the formation of a natural bowl in which rain water had collected. During the space of half an hour in the early afternoon an adult male chimpanzee drank twice. Each time the method was the same: sitting, facing the bowl, he repeatedly put his right hand into the bowl, pulled it out, and, holding it in front of him, licked and sucked the water off his fingers. At various times nine other chimpanzees were in the tree with him, but none drank from the bowl. (Reynolds & Reynolds 1965, 382)

They noted, furthermore, that "this method of drinking appears to be common to all apes" (Reynolds & Reynolds 1965, 382), as it is reported for the gibbon (Carpenter 1964a, 196-197) (see above), the orangutan (Harrisson 1987, 79) (see above), and as shown in the film sequence of mountain gorillas in "Lords of the Forest" (Reynolds & Reynolds 1965, 382). (e) Nishida described the drinking from streams and Lake Tankanyka by chimpanzees of Kasoje in the Mahale mountains of Tanzania. He discerns between drinking sessions, drinking bouts and sucking actions: „A chimpanzee stands quadrupedally, bends down on flexed arms, puts the mouth to the water and sucks it. A drinking bout consists of 1-4 sucking actions [...] and lasts from 8 sec to as long as 10 min [...]. A sucking action lasts from 2 to 50 sec" (Nishida 1980, 190). He noted that in comparison to the chimpanzees of Kasoje, the chimpanzees of Gombe have not been observed drinking from the lake (Nishida 1980, 190) . McGrew communicated to Nishida: "No chimpanzees in Gombe National Park have been seen to drink from the lake. However, chimpanzees have been seen several times to drink form the lake at a spot between the park and Kigoma. This is a very small area containing a few chimpanzees. It is an island surrounded by *shamba* (e.g., cultivated lands). It seems likely that in the dry season, they may have to use the lake, as their small range may not include an ever-flowing stream" (McGrew in Nishida 1980, 205). **(f) The use of tools for drinking seems to occur with chimpanzees. A study at Mahale revealed that the use of leaves or sticks for drinking water has only rarely been observed during a long-term study of wild chimpanzees (*Pan troglodytes schweinfurthii*). However, in**

recent years more than 40 episodes of tool-use for drinking water including more than 70 tools were observed. Interestingly, all of the chimpanzees showing such behaviour were immatures aged from 2 to 10 years. Matsusaka wrote:

> Immature chimpanzees sometimes observed the tool-using performance of others and subsequently reproduced the behavior, while adults usually paid no attention to the performance. This tool-use did not seem to occur out of necessity: (1) chimpanzees often used tools along streams where they could drink water without tools, (2) they used tools for drinking water from tree holes during the wet season when they could easily obtain water from many streams, and (3) the tool-using performance sometimes contained playful aspects. Between-site comparisons revealed that chimpanzees at drier habitats used tools for drinking water more frequently and in a more "conventional" manner. However, some variations could not be explained by ecological conditions. Such variations and the increase in this tool-use in recent years at Mahale strongly suggest that social learning plays an important role in the process of acquiring the behavior. (Matsusaka *et al.* 2006)

(g) In 1965, Jane Goodall reported on several wild animals using "sponges" made of chewed leaves to absorb water for drinking. She estimated this method to be eight times as efficient as the finger-dipping method (Goodall 1965b). **(h) Sponge drinking was not observed in chimpanzees from Kasoje in the Mahale mountains of Tanzania (Nishida 1980).** (i) Sponge drinking was observed by Hunt and McGrew at Semliki in Uganda: „The chimpanzees make and use leaf sponges for gathering water, even when water is easily accessible without a tool. A female sitting on a stone in the center of the Binghi tributary, surrounded by water, was seen to use a wadded leaf to drink water“ (Hunt & McGrew 2002, 43). **(j) In dry seasons, chimpanzees dig holes (wells) in sandy riverbeds and dip water with leaves or leaf sponges (Hunt & McGrew 2002, 46).** (k) Wild chimpanzees at Bossou, Republic of Guinea, West Africa, drank water or absorbed it from tree holes using a leaf (or fibre) as a sponge or spoon. The main users of drinking tools seemed to be females, particularly juveniles and adolescents. Once a chimpanzee was observed using a stick to push a leaf sponge into a water hole and to pull it out again from the hole (Sugiyama 1995). **(l) More than four individuals of M-group of the Mahale National Park, Tanzania, were observed digging into wet ground of a dry stream with their hands to get drinking water (Nishida *et al.* 1999, 150).** (m) Victoria Horner reported on observations during work at a sanctuary in Uganda and at Yerkes National Primate Research: “We sometimes use water from a hose as enrichment with chimpanzees at Yerkes on hot days. Some wet the hair on

their forearms and drink it as it pours off their elbows. Some will hang by their feet from the ceiling of an indoor area and drink upside down, which again appears to be a form of play" (Victoria Horner, pers. comm.). **(n) Sheila Siddle reported a similar connection of drinking and playing in juvenile animals at the sanctuary Chimfunshi in Zambia: "In all our enclosures we have ponds for them to get their drinking water. They are about two feet deep in the middle and we see lots of chimps playing in the water. One will stand there and deliberately splash anyone who is close at hand. They love this game. They also manage to get hold of plastic cool drink bottles and they take them to the pond to refill them" (Sheila Siddle, pers. comm.).** (o) Also J. A. van Hooff, writing on the chimpanzee consortium at the Arnhem Zoo, The Netherlands, reported that suitable objects were used to "scoop up water from the moat, either in play or to drink". Sticks and twigs were used in various ways, e.g., "to 'fish' for floating objects in the ditch." (van Hooff 1973, 202).

4.3.4 Alleged swimming ability in non-human hominoids

apes are generally regarded as unable to swim (e.g., Van Gulik 1967), and captive apes can usually be constrained by deep water moats (Reuther 1976). However, some erroneous statements published in popular media were occasionally reproduced in scientific reviews on primates' interaction with water. For this reason, but also to review the scattered early and modern literature on this topic, the alleged reports on swimming behaviour in apes should be revised here.

Common chimpanzees (Pan troglodytes) and bonobos (Pan paniscus)

(a) In the region of Mongomo in Equatorial Guinea four common chimpanzees (*Pan troglodytes*) were allegedly observed swimming in a dog-paddle fashion across the 60 to 65-metre wide Benito River. This widely ignored observation was made by the Spanish jurist Lois de Lassaletta, who worked temporarily as animal catcher in the former Spanish Guinea (today Equatorial Guinea). Lassaletta reported his observation to the German zoologist Bernhard Grzimek (1909-1987), who regarded the information as reliable enough to be mentioned in a short article in a German journal. Lassaletta stated that he observed the chimpanzees from a boat in the middle of the river. They swam in a dog-paddle fashion (Grzimek 1957). The few primatologists who are aware on this observation (e.g., Reynolds 1967) are inclined to think that the animals were not chimpanzees, but another primate species. **(b) In a German zoology book, an observation of a young common chimpanzee able to swim was succinctly reported by the German zoologist Ingo Krumbiegel (1903-**

1990), without further details (Krumbiegel 1953); Krumbiegel was director of the Zoo Dresden between 1934 and 1936. (c) In a popular book it is mentioned that a male chimpanzee in a rehabilitation island in the Congo River delta began to swim when trying to reach a boat transporting food (Attenborough 2002), without further details or references (but see report below on the swimming common chimpanzee 'Bilinga', which is possibly the same individual as mentioned here). Yann Le Hellaye from the rehabilitation programme H.E.L.P. could not confirm if the chimpanzee mentioned by David Attenborough is 'Bilinga' (pers. comm.). Gavin Thurston, the cameraman who did the film sequences on wading chimpanzees mentioned by Attenborough in the same context of the swimming chimpanzee, confirmed that he filmed the chimpanzees provided by H.E.L.P. in Conkouati, Republic of the Congo (pers. comm.), i.e., in the same place where 'Bilinga' was observed swimming. **(d) Schultz reported that "a few of the many chimpanzees at the zoo in Chester did finally get across the water of broad moats when highly excited", without references or further details (Schultz 1969, p. 45). According to Lynne Ainscough, the moats have developed over 40 years to include hot wire and a smooth wall at the perimeter with an over-hang which would mean that chimps would need to swim to reach this point. Unfortunately, the zoo has no records of dimensions of the moats from this time (Lynne Ainscough, pers. comm.).** (e) The above statement (d) is probably the reason for the following sentence from a website: "Chimpanzees avoid large bodies of water and are usually only able to swim if extremely excited" (Anonymous 2012b).) **(f) Swimming behaviour in two captive chimpanzees was reported in a zoo in Slovenia (Chaput 2012). However, this news journal report turned out to be an April Fool's joke (Jaonlou Chaput, pers. comm.).** (g) Jill Gatwood wrote in a blog about the alleged inability to swim in certain animals. He contacted Tom Silva, the mammal curator of the Rio Grande Zoo in Albuquerque, New Mexico, and asked him about swimming ability in apes: "According to Tom, most large primates such as gorillas and orangutans cannot swim, partly because their centers of gravity are in their necks and sternums. 'They sink like stones,' says Tom. He says he has seen chimpanzees swim, though"(Gatwood 2000). Attempts to contact Tom Silva – he has retired from the Rio Grande Zoo (Terry Axline, pers. comm.) - were unsuccessful. **(h) The only alleged observation of swimming bonobos (*Pan paniscus*) concerns wild animals: the Mongo people of the Democratic Republic of the Congo reported to a primatologist that bonobos can swim, an assertion that was interpreted as "far from believable" (Kano 1992).**

Orangutans (Pongo pygmaeus)

(a) In a popular book the word “swimming” was used to describe what seems to be Bornean orangutans (*Pongo pygmaeus*) sitting, wading or hanging on trees in breast-deep water at a rehabilitation island, Kaja, in the province of Central Kalimantan, Borneo (Schuster *et al.* 2008). **(b) An orangutan was observed and photographed after momentary loss of upright posture during wading (Russon *et al.* 2010a), a behaviour which was in popular media inaccurately termed “swimming” (Derbyshire 2009).** (c) According to reports published by Russon and collaborators, three juvenile orangutans were observed when gliding or showing rudimentary paddle over a short distance (Russon *et al.* 2010b). Although this report does not provide further details, it indicates that orangutans are able to perform what can be regarded as preliminary stages of a fully developed swimming ability.

Gorillas (Gorilla gorilla)

(a) The first broad review of water use and swimming ability of apes was published in 1929 by Robert and Ada Yerkes. They summarised the evidence to date on this subject (here quoted from a later edition):

> Granting the inconclusiveness of the evidence we venture the tentative inference therefrom that the gorilla possesses neither fondness for water as a surrounding medium nor natural ability to swim. In these respects we have discovered no reason to suppose that it differs essentially from man, orangutan, or chimpanzee. Whether like man the great apes can readily learn on their own initiative or be taught to swim we do not know. (Yerkes & Yerkes 1945, 410)

(b) In an early report, the prints of a herd of eight west lowland gorillas at a riverside in Cameroon were interpreted as evidence that they had swum across this river which in that place was sixty meters broad (von Oertzen 1913). (c) The zoologists Richard Lynch Garner wrote in 1896: "I have been told that the gorilla can swim, and it may be true; but I have never observed anything in his habits to confirm this, while I have noted many facts that controvert it" (Garner 1896, 125). **(d) Cousins reported on the young male gorilla ‘Arthur’ at the Primate Centre in Makokou, Gabon, who was “thought to swim” in the employers’ swimming pool by P.J. H. Van Bree, curator of the department of mammals, Amsterdam Zoological Museum (Cousins 1978, 11). However, Wim Bergmans from the Amsterdam Zoological Museum, questions if the gorilla was really able to swim. Bergmans knows Van Bree personally, and had heard different versions of this story**

from him over the years. He suspects that the gorilla was just playing in shallow water (Wim Bergmans, pers. comm.). (e) The behaviour of two gorillas playing intensively (but, as we will see, definitively *not* swimming) in the shallow part of a water moat in an exhibit at the University of Ibadan Zoo in Nigeria (Golding 1972) is sporadically mentioned as an example of swimming gorillas (see below). As it will be demonstrated, this error is related to a misinterpretation of some of Golding's statements.

Golding's report on the gorillas' behaviours toward water is presented here in detail, often largely quoted verbatim, for two main reasons. On the one hand, these gorillas show a degree of interaction with water that is unknown in wild and captive apes, with exception of the chimpanzee 'Cooper' and the orangutan 'Surya' (chapter 4.4). It is therefore important to understand all available factors which influenced the development of intensive water use in these two gorillas. On the other hand, Golding's verbatim quotations are necessary to compare with some erroneous statements which were mistakenly attributed to Golding.

Golding spent many years working with animals in West Africa, first in Cameroon in 1957, then developing the Zoological Garden at the University of Ibadan, Nigeria, from 1963 to 1979 (Golding 2010b). In 1967, he wrote about the problems he faced in providing new accommodation for the two young gorillas (the male 'Aruna' and the female 'Imade') and a trio of chimpanzees. According to Golding, there were brought illegally into Nigeria from Cameroon and were offered for sale to the University of Ibadan Zoological Garden. After consultation with the Nigerian Federal and Cameroon Governments, the zoo was allowed to confiscate the two gorillas from the Asian traders (Golding 2010a). Both animals had been badly treated prior to arrival, which was evident in the their aggressive and nervous behaviour and physical condition (the young male was burned on the chest); the gorillas arrived at the zoo on 18 December, 1964 (Golding 2010a). Golding did not know exactly where the gorillas originated from. He wrote: "[W]e assumed them to be western lowland gorillas (*Gorilla gorilla gorilla*). However, a distinct subspecies from the Nigeria Cameroon border area was formally described and named the Cross River gorilla (*Gorilla gorilla diehli*) in 2000" (Golding 2010a). When arrived at the zoo, it was estimated that 'Aruna' was 2,5 years old and 'Imade' around 1,5 years old (Golding 2010a). In 1967 Golding "realised that serious thought was needed regarding the future of the two gorillas. The type of ape accommodation that I found at the zoo when I arrived [...] was old, badly designed and totally unsuitable. If the gorillas were to remain at the Zoo, a new building was required incorporating the latest

concepts in zoo design" (Golding 2010a). In 1972 he published an article in the International Zoo Yearbook, on the design and construction of the new ape building, and the unusual gorillas' behaviour towards water (Golding 1972, 71). Although other observations of intensive water use in gorillas were published, this paper remains the most interesting and unusual description of behaviours towards water by captive gorillas.

The main problem concerned the design of the outside accommodation. He planned to provide "as large an area as possible for each group of apes in order to maintain the animals in satisfactory physical and mental health" (Golding 1972, 71). After he rejected several ideas because the costs or other reasons, he came "somewhat reluctantly" to the conclusion that the best solution would be a water-filled moat. He wrote:

> I was reluctant for two reasons; first, there had already been accidents in other zoos involving all three species of great apes when animals had entered the water for one reason or another and drowned, and secondly, because our two gorillas had already shown signs of positively enjoying water. On hot days they loved nothing more than to be drenched with water from the hose pipe, becoming very excited and boisterous in the process, although I had noticed that our chimpanzees carefully avoided bodily contact with water at all times. (Golding 1972, 71)

He described the moat's design and his concerns about the gorillas' and humans' safety:

> It seemed necessary to divide the moat into two sections, with the section on the animals' side separated from the remainder in such a way that if the apes entered the water, either deliberately or accidentally, they would be prevented from rolling across into deeper water and would be able to scramble back to safety easily. On the other hand, it also seemed important to have the section accessible to the animals sufficiently deep and wide to maintain their respect for water even if, as I suspected might happen in the case of the gorillas, the animals became accustomed to it and entered deliberately. Thus, if this latter situation developed, I hoped to minimize any desire on the part of the apes to cross to the other, deeper section. The wider, deeper section on the visitors' side was a necessity in case the animals, when adult, did somehow manage to cross from the near section. I considered it preferable to have a drowned gorilla to an escaped gorilla, especially in such a sensibly populated area. (Golding 1972, 73)

He described the dimensions of the moat and technical installations designed to prevent the gorillas drowning (the ground plan of the exhibit is depicted in (Golding 1972, 72), the crossing section of the moat in (Golding 1972, 74):

> The floor of the moat was therefore designed to slope down fairly steeply from the inner side to a horizontal distance of 1.4 m. At that point a 30 cm high wall is built along the floor of the moat, parallel with the sides, into which are concreted a series of uprights supporting three horizontal underwater rails.[...] The water at this (deepest) part of the section available to the animals is 1.06 m deep if the moat is full. Should one of the apes find itself in difficulty here, the 30 cm wall prevents the feet and legs of the animal from slipping under the bottom rail, and provides a firm base against which it can thrust with its feet to gain dry land. The rails, as well as acting as a barrier, also provide firm hand holds. The moat floor, from the inner edge to the wall and rails, has a roughened surface to prevent the animals from slipping and also has two 3.1 cm high raised ridges running parallel with the edge to provide additional finger and foot holds. (Golding 1972, 73)

The completed compounds were finished in March 1970. In the expectation that the animals, particularly the chimpanzees, would be excited when first released and might behave erratically, Golding adjusted the water level in the moat so that in the inner section it was only a few centimetres deep, preventing accidents in the water moat and giving the animals "easier access to the electrified wire which I wanted them to experience for its unpleasant properties as early as possible" (Golding 1972, 73-74). Golding describes the behaviour of the three chimpanzees (one male and two females) after they were finally released from the building into the completed compounds:

> When the adult male chimpanzee emerged for the first time into the compound he was in a highly excited and aggressive state with all his body hair erect. He walked around the compound briefly, then went down the side of the moat into the shallow water and grasped the wire, obviously with the intention of climbing over. He immediately received a shock, screamed, and then retreated with his body hair rapidly subsiding. He looked up at me in such a way that I knew he wanted to be held and comforted. He again tried to cross the wire, apparently in an attempt to reach me (although of course this would have been impossible because of the deeper water on the other side), and again received a shock which evoked another loud scream. This happened perhaps six times in the space of a few minutes, after which he rushed back, still screaming, to the far corner of the compound where he sat motionless for a long period. From that day on, whatever the depth of the water, he has never attempted to leave the edge of the moat. (Golding 1972, 74)

The females behaved differently. Golding wrote: "The two young females were more cautious in their initial explorations but each nevertheless soon touched the wire and received a shock.

They, too, have never since attempted to leave the edge of the moat although one of them very occasionally stands with her feet and ankles in the shallow water at the edge itself, carefully holding on to the raised concrete kerb all the time" (Golding 1972, 74). Golding was convinced that "all three chimpanzees remember these unpleasant incidents of the first day, but apart from this they have also kept their basic dislike of water, and except for the rare occasions just mentioned have never bodily entered the moat deliberately or accidentally. Even if one of them were to fall in accidentally I am convinced that it could either scrabble back or hold on to the underwater rails and stand up with its head above water" (Golding 1972, 74).

Golding described in detail the gorillas' behaviour after they were released in the moated enclosure:

> The gorillas [...] were also initially cautious and moved around their compound inspecting their new surroundings with great deliberation. Their self-confidence soon increased however, as did their chest-beating, and eventually both climbed down into the moat and grasped the wire. The reaction of the female was to retreat immediately, accompanied by a low whimper and frequent puzzled glances over her shoulder at the wire. She has since done her utmost to avoid contact with the wire and has certainly made no attempt whatsoever to cross from the inner moat section. (Golding 1972, 74-75)

Golding described the reaction of the male towards the wire:

> The reaction of the male, on receiving a shock, was to screw up his face and duck as though he had been attacked from above. He climbed back to the moat edge and moved around there, sitting down frequently and staring at the wire. After a few minutes he again went down and reached out and then withdrew his hand several times before his fingers eventually made contact with the wire and he received another shock. Again he ducked and retreated, and after a few more stares renewed his inspection of the compound. (Golding 1972, 75)

Golding maintained the low water level for some days, and with a keeper constantly watching the gorillas. Then the moat was emptied for a structural inspection and afterwards filled to near the maximum water level. Golding described the gorillas' behaviour in this environment:

> Within a few days of having access to the maximum water depth in the inner moat section, both animals were entering the water with tremendous enthusiasm. They sat on the bottom of the moat with the water up to their chins, always taking care not to submerge their faces below

> the surface. As their confidence increased they began to beat at the water with their hands, delighting in the variety of noised that could be thus produced and standing up frequently, with water pouring off their bodies, to beat their chests violently and then submerge again. (Golding 1972, 75)

The gorillas began to show what can be called a preliminary stage of rudimentary swimming movements in a sitting position in shallow water. Golding wrote: "With the water up to their necks they were, of course, very buoyant and soon they began to propel themselves along in a sitting position - their faces just above water - by pushing their hands and feet against the underwater rails and moat bottom. They took great pains to avoid the electrified wire, soon becoming adept at moving along the moat with just 5 to 8 cm separating them from it" (Golding 1972, 75).

The gorillas soon began to show other interesting behaviours in the water. Golding wrote: "Their prowess in the water developed rapidly and it was only a week or so before the male was able to launch himself with a kick from the moat bottom, travelling several feet in a horizontal 'breast-stroke' position with arms out straight in front of him, before slowing down and kicking out from the moat bottom again. He also launched himself by pulling with his hands against the underwater rails" (Golding 1972, 75). As shown below, this passage was later misinterpreted as gorillas being able to swim using a breast-stroke. Furthermore, both gorillas began to show a similar behaviour as later observed in wild western lowland gorillas (*Gorilla gorilla gorilla*), that used water to generate spectacular splash displays in swampy areas, mostly displayed by silverbacks in an agonistic context (Parnell & Buchanan-Smith 2001a; Parnell & Buchanan-Smith 2001b). Golding wrote: "Both animals soon learned to run across the compound and either leap diagonally into the water in a tremendous belly-flop or twist around at the last minute and plunge in backwards, all the time being careful not to submerge their faces. They took turns in chasing each other along the edge of the moat, the one behind attempting to push the other into the water" (Golding 1972, 75).

Within a few days of being outside, the male gorilla found a way to access the deeper part of the moat:

> [Aruna] discovered that by lying flat on his stomach he could squeeze sideways between the top rail and the electrified wire without touching the latter. Further, he developed a technique of squeezing between the top and centre underwater rails by carefully passing first his legs

> then his body between the rails and moving across until only his head was left above water. Then very quickly he pulled his head under the water and between the rails to the other side, grimacing furiously on surfacing. Having crossed to the deeper section by one method or the other he then walked sideways up and down the moat, hanging on the top rail as he did so, he was able to regain the inner section by jumping clumsily back into it from the top rail at the bend of the moat, where the electrified wire ran somewhat inside the curve of the rail instead of being directly above it. (Golding 1972, 75)

Both methods of crossing the barrier were easily stopped with some technical corrections. Golding wrote:

> Alternate rods supporting the electrified wire were removed and replaced by another set of supports consisting of lengths of 2.5 cm (1 in) galvanised tube projecting above the maximum water level to a height of 45 cm (18 in). Three hooks were welded to each new support and it was thus possible to suspend three wires one above the other with a narrower space between the bottom one and the top underwater rail. (Golding 1972, 75)

With these modifications, the male was unable to cross the new barrier and "soon showed no further interest in the matter" (Golding 1972, 75). One year after the compounds have been in daily operation (June 1971), all the apes are in good health (Golding 1972, 76). Golding reached a very positive conclusion on the gorillas' intensive interaction with water:

> The major fascination continues to be the gorillas' astonishing use of water, and there is no doubt that the availability of this medium had added a whole new dimension to their activities. They are regularly inspected and appear to have suffered no ill effects from their frequent contact with water. At first I thought that perhaps the animals' skins might be affected in some way but so far my fears have been proved groundless. Another possibility was that the water would be effective in harbouring and passing on unusual levels of bacterial and parasitic infections but indications to date are to the contrary, although there is yet time for further evidence. (Golding 1972, 76)

Golding's fear that the gorillas would become chilled has not been confirmed, as "they appear able to judge the situation perfectly well, and on cool days and during much of the rainy season they enter the water less frequently than on warm days. The development of colds is now a rarity compared with the period when the animals had no access to adequate outdoor exercise" (Golding 1972, 76). Golding stated that the environmental settings might be reconsidered when the animals breed and small infants are present in the compounds. For

instance, as he wrote, “it may be necessary to adjust the water level or carry out certain modifications. However, for the time being we have solved most, if not all, of the problems both envisaged and encountered and have created an exhibit that has not only attracted great interest but which I believe will result in the satisfactory development of both groups of apes” (Golding 1972, 76).

In December 2010, Golding answered several questions about the further development of the gorillas’ and chimpanzees’ interactions with water in the Ibadan Zoo. The author was especially interested in a possible further development of the aquatic skills of the gorillas, of the water use in young gorillas or chimpanzees (in cases where they had reproduced in the zoo), and in accidents or other significant events related to water use in these and other primates. Golding replied that neither the gorillas nor chimpanzees were old enough to breed during his time there, and that the gorillas did not develop any further skills in water. The chimpanzees’ reluctance to enter into the water did not change from the situation he described in his article. He wrote:

> I had chimpanzees in a compound bounded by exactly the same moat design as for the gorillas. However, the chimps seemed to dislike the water and avoided it, with the exception that I describe. It must be remembered that both the gorillas and the chimpanzees experienced electric shocks soon after they were allowed access to the moats, but whereas the gorillas subsequently learned to 'go back' and use the water but avoid the electrified wire, the chimps even avoided going into the water. (Robert Golding, pers. comm.)

Unfortunately, Golding’s precise report led to several erroneous statements propagated in the literature. Since these erroneous statements were expressed not only in the media but also in the few scientific reviews on primates’ interaction with water, it is necessary here to identify their sources.

In the popular media, the gorillas were often described as able to swim. For instance, following text is written as a caption on the back of a press photo (author’s collection):

> GORILLA APES HIS KEEPER – AND LEARNS TO SWIM. Water play is not something gorillas enjoy: in fact, they have an aversion to it, Aruna, a 7 year old gorilla at Nigeria’s Ibadan zoo, is an exception to the norm – she [sic, he] loves the water, and is learning to swim by copying the movements made by her [sic] keeper. [...] I’ll show you how to swim; just do as I do.

The sentence above "learning to swim by copying" humans movements is not corroborated by anything mentioned in Golding's article. As we will see in chapter 4.4.3, it is often erroneously assumed that apes will only be able to interact intensively with water (e.g., to submerge large parts of the body in water or to swim) if taught to do so by humans or by imitating a human. Despite the fact that the gorillas in the Ibadan Zoo were not swimming, they acquired their behavioural novelties after being released in the moated enclosure. In his article and in his personal communication to the author, Golding did not mention that any sort of "swimming lessons" took place in the zoo.

More seriously was the fact that Golding's statement on the male gorilla gliding in water was misquoted by Elaine Morgan in her book *The Descent of Woman*. Morgan wrote:

> It is a well-known 'fact' that chimps and gorillas are non-swimmers and any zoo could safely keep them in an un-walled enclosure by building a shallow moat around it. If by some accident they fell in, they would panic and drown. But now hear Robert Golding, zoo curator at a Nigerian university, reporting on two gorillas aged six and half and seven years old. (Morgan 1972, 33)

Morgan then quoted following passage:

> 'The female in particular enjoyed having water hosed over her. When allowed access to the moat she went right into the water. The male was at first cautious but seeing her enjoying it, he followed. They now stand in the deepest part, up to their middles, and launch themselves forward in a sort of breast stroke. They do this many times a day. ... Seeing a man swimming on the other side of the barrier, the gorilla launches himself in a horizontal position with his arms straight ahead of him. It seems to come to him quite naturally' (Golding [sic] in Morgan 1972, 33, single quotation marks from Morgan)

Asked about this passage, Morgan did not remember from where she had got it from (Elaine Morgan, pers. comm.). Although this passage is definitively based on Golding's report, the following facts exclude the possibility that Golding is the author of this specific statement (what would be possible, however, is if the passage was quoted from an interview published in a newspaper, since the story was widely presented in the media). (1) The statement assuming that "the female in particular enjoyed having water hosed over her" is probably wrong, since no such gender specific behaviour was described by Golding, although he was very gender specific when referring to all behaviours towards water in these gorillas. Golding

wrote: “On hot days they loved nothing more than to be drenched with water from the hose pipe, becoming very excited and boisterous in the process” (Golding 1972, 71). (2) Similarly, the passage in Morgan’s book “The male was at first cautious but seeing her enjoying it, he followed” is not compatible with several facts described by Golding. For instance, following statement suggest that the male was less reluctant to interact with new aspects of the environment than the female: “While both Aruna and Imade soon settled well into their new home and routine, and related well to their keepers, it soon became apparent that Imade [the female] was much more suspicious than Aruna of any new or strange items that entered her domain” (Golding 2010a). This view is supported by another statement: “the male, Aruna, was more resourceful and adventurous than Imade” (Golding 2012). In his article, Golding described the male – although he also experienced shocks by touching the wire – as less reluctant to approach the fences. Therefore, only the male submerged his head to pass under the underwater rail to access the deep water moat, and only the male was travelling several feet in a horizontal position . (3) There is a further crucial deviation between Morgan’s and Golding’s statements. Golding’s original sentence: “the male was able to launch himself with a kick from the moat bottom, travelling several feet in a horizontal *‘breast stroke’ position* with arms out straight in front of him, before slowing down and kicking out from the moat bottom again” (Golding 1972, 75, italics added) is transformed in Morgan’s book as “they [sic, as only the male showed this behaviour] launch themselves forward *in a sort of breast stroke*” (Morgan 1972, 33, italics added). While Golding’s breast-stroke position refers to a similarity between the *position* adopted by the gorilla and a human during swimming, the passage published in Morgan’s book wrongly suggests a similarity in the *swimming technique* used by the gorillas and humans. However, Golding was careful never to state that the gorillas could swim (Golding, pers. comm.), as the male was gliding after kicking out from the moat bottom.[59] It is impossible that Morgan’s text refers to the gorillas’ behaviours developed after the publication of Golding’s article, since - according to Golding (pers. comm.) - the gorillas did not later develop any aquatic skills other than those described in his article. (4) Finally,

[59] In another passage, Golding described the gorillas propelling themselves “along in a sitting position” (quoted above, chapter 4.3.3). This sentence implies two possibilities: either the gorillas were moving by pushing with their hands on the ground, or they were moving by swimming movements. In the latter case, this almost implies that they used a kind of breast-stroke movement with the arms. In any case, these astonishing behaviours cannot be interpreted as “swimming” in the sense of the definition used here (see chapter 4.1.3), which exclude “progress in water by pulling or pushing something else than water”. Furthermore, the passage on “breast stroke position” was mentioned by Golding in another context and should not be merged with the passage discussed here.

the sentence by Morgan "Seeing a man swimming on the other side of the barrier, the gorilla launches himself in a horizontal position" is a story freely constructed out of one of the pictures from Golding's article, in which a man standing in water is giving a leaf to one of the gorillas standing on the other side of the fence. This statement might be influenced by free (and wrong) interpretations which were published in the media at this time (see above).

To summarize, it is reasonable to assume that the passage in Morgan's book was formulated by Morgan[60] based on Golding's article, and the statement was mistakenly reproduced as a verbatim quotation. Since Golding's paper was for decades difficult to access, the verbatim quotation in Morgan's book was the only source of Golding's report, and this led to statements on gorillas as able to swim in the few reviews on primates' interaction with water (Ellis 1987; Kempf 2009).

Gibbons (Hylobatidae)

One of the most widespread unconfirmed assumptions on swimming apes concerns the siamang (*Symphalangus syndactylus*).

(a) In a Spanish popular zoological encyclopaedia it is stated that the siamang "also diverge from their relatives in the sense that they are able to swim [*nadar*] with relative ease", without further details or references (Fuente 1970, 59). **(b) In a book on human evolution it is succinctly written that the siamang "is clumsy in the trees [*sic*] but (unlike the other apes) it is able to swim" (Birx 1988, 133), without giving further details or references.** (c) In a popular German zoological lexicon it is stated that siamangs are able to swim across streams using "a kind of breaststroke" [*eine Art Bruststil*] (Anonymous 1982, 62), without giving further details or sources. **(d) A similar statement was made on a website on siamangs: "siamangs also can swim rather well, using a breast stroke and keeping their heads well above the water", without giving references (Ismail 2004).** (e) Several similar statements on swimming siamangs can be found on other websites, for instance in (Anonymous 2012e; Klein 2012), without giving further details or sources. **(f) The ornithologist Jean T. Delacour (1890-1985) reported own observations on captive gibbons: "If they fell into the water, they would immediately swim to reach the nearest shore, but they never take to water willingly, and I proved with captive animals kept at my home near Clères, France, that a**

[60] Morgan's sentences on the female as more aquatic than the male is also compatible with the general ideas defended in her book *Descent of Woman* - in this time she defended a feministic view on human evolution (see Appendix D).

ditch 3 m wide, filled with water, is an obstacle that they will not cross" (Delacour 1933). From the above statement it is not clear if the animals came out of the moat after falling very close to the shore (for instance after pushing with the feet on the ground) or by swimming movements in deep water over a considerable distance. (g) A more detailed observation was provided by Thomas Geissmann (primatologist specialised in gibbons) when he tried to get pictures of one adult gibbon pair (*Hylobatidae muelleri* hybrids) kept on an island in the former German Democratic Republic in 1988. For unknown reasons, the female (but not the male) got quite agitated when she saw him:

> She presented to me repeatedly. From the context, I was unable to determine whether this behaviour was a friendly or an aggressive gesture (both explanations would have been possible in that situation). She run up and down the shore opposite to my position, apparently trying to get across the pond. Finally, she actually jumped in the water. […] She immediately climbed out of the water at the same spot where she jumped in. Water contact time was about 2 seconds. I am not sure whether she was able to reach the ground at the place where she jumped into the water, or whether she actually swam for a second. In any case, she seemed to have cooled down after the bath and rejoined her climbing scaffolding. She did not come back to the shore and she did not present to me again. (Thomas Geissmann, pers. comm.)

(h) Frank Finn edited and revised the book *Natural history of the Mammalia of India and Ceylon*, originally written by Robert A. Sterndale. This new edition was published under the title *Sterndale's Mammalia of India: A new and abridged edition, thoroughly revised and with an appendix on the Reptilia* (Sterndale & Finn 1929). In the chapter describing the "Rhesus monkey or common Bandar" (*Macaca mulatta*), Finn describes the readiness of the Rhesus macaque to take to water (see chapter 4.2.4), adding following remark: "The biped Gibbon is unable to swim, like untaught man, and throws up its arms in the same way (Finn, in Sterndale & Finn 1929, 17). (i) Parsons wrote the following on gibbons (*Hylobates hoolock*) in the journal of the Bombay Natural History Society (BNHS) "My observation shows that they seem to dislike having to swim in order to cross a river of any size, or, of course, it may be that it is a dislike of coming to earth from the trees" (Parsons 1941, 434). He pointed out that gibbons seem to be absent in certain areas suited for this species, and concluded that rivers seem to form a complete barrier to the spread of this species. Following statement to Parson's report was added by the editors of the journal: "Rivers when they are wide enough definitely form natural barriers to certain groups of

monkeys. Macaques readily take to water, but gibbons and leaf monkeys (*Semnopithecus*) appear to have an aversion to water and are usually baulked by a river. Nevertheless both gibbons and leaf monkeys can swim. Mr. McCann tell us that when on the Chindwin Expedition, he put a baby gibbon on a raft to prevent it becoming a nuisance, but it deliberately jumped into the river and swam ashore" (J. F. Caius, H.M. McGusty and S.H. Prater, in (Parsons 1941, 434).

This observation is astonishing for several reasons. Firstly, insofar as can be assessed, unambiguously swimming behaviour in gibbons was never observed by other primatologists.[61] Secondly, as already shown, the statement on swimming gibbons is contradictory to single observations on the lack of swimming ability in gibbons reported by specialists. On the other hand, "McCann" mentioned by the editors refers to Yale Mervin Charles McCann (1899-1980), an Indian naturalist with an outstanding reputation (Abdulali 1980). He was well known by the editors of the journal of the BNHS, as he was an associate of this society and published mainly in the same journal. The fact that some statements on swimming gibbons include the details on the mode of swimming (e.g., Ismail's assumption of gibbons using a breast stroke and keeping their heads well above the water, and others) is at least striking. These statements may be interpreted in at least three ways: (a) one or more of these statements are based on factual observations; (b) they are based on an early source (unknown to this researcher) in which specific swimming movements in gibbons is reported (but not McCann's observation, which does not give details on "swimming technique" in gibbons); (c) all the statements on swimming gibbons are the product of imprecise information, inadvertent or deliberate misinterpretations. The way how such misinterpretations can be propagated in the literature has been demonstrated in the above-mentioned cases of alleged swimming behaviour in gorillas and orangutans, and in some of the alleged swimming behaviour in chimpanzees (e.g., swimming chimpanzees when excited (Anonymous 2012b) and the April Fool's joke by Chaput).

Conclusion on alleged swimming ability in apes

In all of the cases above, the most intriguing are the reports by de Lasseta, Krumbiegel and Attenborough (all on chimpanzees), and the statement on a swimming gibbons by Delacour and McCann. The vague and succinct nature of these statements (or, in the case of Lasseta's

[61] For instance, a specialist in gibbons wrote: "I have never seen or heard of gibbons swimming over the last 40 years" (David J. Chivers, pers. comm.).

observation: the large distance between observer and the swimming primates) does not allow what may be called a “definite confirmation” of swimming activity in apes. However, the lack of conclusive direct or indirect evidence on swimming behaviour in apes does not necessarily mean that swimming behaviour should be completely excluded as a possible output of intensive interaction with water in wild or captive apes. It is important to note that the common opinion stating that apes do not have the anatomic pre-conditions necessary for the development of swimming ability (see the low fat hypothesis by Angus, chapter 6.8.1) is strongly influenced by data gathered on captive animals in conditions designed to minimize interactions with water bodies (see chapter 4.3.6).

The alleged observation of swimming wild bonobos from the Mongo people of the Democratic Republic of the Congo reported to Kano is difficult to evaluate. Although bonobos are generally considered as less reluctant to enter water than other apes and show, in some cases, extremely frequent interactions with water in semi-free ranging conditions (as in the Lola ya Bonobo Sanctuary, see chapter 4.3.3, passim), these bonobos “have never been observed to swim or attempting to swim” (Zanna Clay, pers. comm.). This is confirmed by Vanessa Woods, who works at the same sanctuary and had opportunities to observed several bonobos interacting intensively with water. She stressed the fact that bonobos in this place only go in water while their feet can touch the bottom, and swimming behaviour does not occur (Vanessa Woods, pers. comm.).

In summing up, insofar as it can be assessed, alleged observations of gibbons, orangutans, gorillas, chimpanzees and bonobos swimming deliberately over a distance of more than one metre are not confirmed by video footage, sequences of photos, experiments, observation by different reliable witnesses or other forms of scientific evidence. However, some of the above statements on swimming apes (especially on chimpanzees and gibbons) are striking and it cannot be completely excluded that they might be based on factual observations – this is especially true when taking into consideration the reported described in the next section.

4.3.5 Unconfirmed but reliable reports on swimming and diving in common chimpanzees

Here are presented reliable reports on the swimming of two common chimpanzees (one captive and one semi free-ranging), one case of an unknown form of underwater locomotion in a captive common chimpanzee, and a report on swimming in a captive orangutan (the behaviour was captured on video, but this material is still not available to me) . The following

criteria were here used to define a report as "reliable". First, the behaviour was repeatedly observed close-up by one or more persons working regularly with chimpanzees in captive or semi free-ranging settings and they were therefore able to accurately identify the observed species. Second, the animal was undoubtedly observed while swimming in deep water, clearly beyond wading depth, and the observation explicitly excludes holding onto branches, occasionally pushing with the feet on the ground or any other form of behaviour not compatible with our definition of swimming (see above). The only potential exception to the last criterion concerns the common chimpanzee, Barbara (see below): she moved under water with poor visibility and no observation on the mode of propulsion was possible.

'Barbara'

The female common chimpanzee 'Barbara' (1973-2005) was kept in the Lion Country Safari, a private zoo in West Palm Beach, Florida. The presented evidence is based on interviews with the zoo director Terry Wolf who directly observed the behaviour. Almost nothing is known about the conditions in which 'Barbara' was kept in captivity before she came to the zoo. In the Lion Country Safari, 'Barbara' was kept with other chimpanzees on islands separated from the land by a canal averaging 10,5 m wide. The canals were man-made, but without the use of concrete, with vegetation at the shore and in the water. On August 2010, different chimpanzees were observed several times by the zoo staff going to the canal and sitting in chest-deep water – apparently for thermo-regulatory purposes. 'Barbara' was able to escape at least three times from the island where she was living (Terry Wolf, pers. comm.). At the place where 'Barbara' crossed the canal, the water reaches a depth of *ca* 1,8 m at a distance of about 3 m from the island shore. The gentle slope of the canal allowed 'Barbara' to wade about 2,5 m from the shores on both sides; and 'Barbara' was observed crossing the remaining 6 m under water (Terry Wolf, pers. comm. and interview on August 19, 2010). As 'Barbara' was fully submerged and the water had poor visibility, it can only be speculated how she moved under water. It is possible that 'Barbara' pulled on the vegetation on the bottom or swam under water, or used a combination of both methods. Owing to the impossibility of keeping her on the island, she was transferred in 1991 to another zoo in North Florida without water moats, where she died in 2005.

'Shasa'

The female common chimpanzee, 'Shasa' (born approximately in 2004) is kept in the sanctuary J.A.C.K. (*Jeunes Animaux Confisques au Katanga* / Young animals confiscated in

Katanga) in Lubumbashi, Democratic Republic of the Congo. The presented evidence is based on interviews with the person who directly observed the behaviour, Roxane Chantereau. 'Shasa' arrived at the sanctuary in July 2006 when she was about 2,5 years old after she was confiscated in a market in Kinshasa, DRC. She lost her left eye during seizure. No information is available about where she was captured in the wild or about the captivity conditions previous to being rescued from a trader. When she arrived, the sanctuary was on a small island at the Lubumbashi Zoo. To the astonishment of the personnel of J.A.C.K, 'Shasa' was able to escape from this island by swimming over a 2 m deep x 3 m wide moat. This was not a single event, since she escaped regularly (many times a day). No interaction with humans in water occurred at the sanctuary in this time or later (Roxane Chantereau, pers. comm.). In the place she is kept now with other chimpanzees, she has access to a pond and uses it regularly. After concerns related to the possibility that other chimpanzees might follow 'Shasa' and drown, a rock was placed in the middle of the pond (Roxane Chantereau, pers. comm.). Video footage of this pond (albeit with a very low water level) can be found in (Anonymous 2009a; Anonymous 2009b).

Video footage of 'Shasa''s swimming behaviour was not possible, since every time Chantereau approached the chimpanzees to film, all of them immediately approached her in the expectation of food (R. Chantereau, pers. comm.). In the time I received the first personal communication (July 7, 2010), it was reported that 'Shasa' was the dominant female, and that "she still likes going into water" (R. Chantereau, pers. comm.). "'Shasa' doesn't stay for hours [in water]; maybe 15 to 20 minutes several times (3 to 4 times) a day, especially when the weather is very hot (from September – October – November). During our winter (April through July-August) she doesn't swim as it is too cold" (R. Chantereau, pers. comm.). 'Shasa' was never observed putting her face under water, although she "doesn't mind standing outside in a pouring rain" (R. Chantereau, pers. comm.). According to Chantereau, 'Shasa''s behaviour certainly influenced the behaviour towards water of two other chimpanzees: when the weather is extremely hot, "the two others are no longer scared of water and walked in the pond until water reaches their hips. They don't go further or can sometimes sit in the water and put water over their heads" (R. Chantereau, pers. comm.). In December 2010, Chantereau observed that 'Shasa', although apparently in excellent health, was interacting less with the water in the pond. Chantereau thinks that this could be the result of hormonal changes occurred after she received a contraceptive implant in July 2010 at the

age of 6 to 7 years, when she started her first heats. Although Chantereau did not observe 'Shasa' swimming at this time, this behaviour was observed by other workers at the sanctuary (R. Chantereau, pers. comm.).

'Bilinga'

The male common chimpanzee 'Bilinga' (born in 1993) lived in semi free-ranging conditions on an island in Conkouati, on the west coast of the Republic of the Congo. The presented evidence is based on secondhand testimony. As part of a rehabilitation programme called H.E.L.P. Congo (*Habitat Ecologique et Liberté des Primates du Congo*), the chimpanzees are daily provided with supplies of food transported by boat. In an attempt to reach the boat before the other chimpanzees, 'Bilinga' was repeatedly observed swimming towards it, always in the proximity of branches (less than 1 m), but without any support. The behaviour was observed in 2001 (Yan Le Hellaye, pers. comm.). Le Hellaye, who works in the rehabilitation centre, did not himself observe 'Bilinga' swimming, but reported the observation of another person who supplied the chimpanzees with food (Yann Le Hellaye, pers. comm.).

An orangutan in the Singapore Zoo

Professor emeritus Joseph Erwin, after reading the description on Suryia's and Cooper's swimming and diving behaviour (Bender & Bender 2013), sent an email to me on 17 August 2013,[62] where he wrote: "For years I have been telling people about an orangutan I observed swimming in the moat of his/her enclosure at the Singapore Zoo, but most of the colleagues I mentioned this to seemed to not believe me or try to explain it away. I did video record this". According to him, "the orangutan was doing a sort of modified side stroke (which actually kind of resembled the stroke of the one you have the video of) – but in the Singapore Zoo case, the orangutan was reaching out with the lead arm and catching handfuls of tiny fish that swam in clustered schools in the moat. So, the fish eating was also an interesting aspect of the behavioural pattern, and may well have provided the incentive for learning to swim in this case" (Joseph Erwin, pers. comm.).

[62] For some reason, the email came through only five months later (on 14 January 2014).

4.3.6 Discussion on aquatic activities in apes

Overall discussion

The present review confirms the common assumption that all hominoid species lost the instinctive swimming ability, and to cross water bodies is a difficult task for them. Data of the review show that different techniques are used by apes to cross water bodies in the wild, in semi-free ranging conditions and in zoos. Although all apes will probably always prefer to use natural bridges to cross water bodies, different alternative techniques occur in the absence of such bridges. In free and semi-free ranging conditions, orangutans seem not to avoid wading in shallow water; they were repeatedly observed using natural bridges or sticks to improve the balance in water and/or to probe the water depth. Wild gorillas, in the absence of natural bridges, seem to avoid crossing. Exceptions are western lowland gorillas visiting bais. Their large bodies and terrestrial adaptations are obvious constrains to the use of the canopy to cross water bodies. Chimpanzees cross water bodies stepping on stones or fallen branches that rise above the water surface, or by jumping. They can also cross through the canopy. The use of floating devices to aid crossing water bodies was observed only in orangutans and chimpanzees in sanctuaries and zoos, but not in the wild.

Wading was observed in gorillas, chimpanzees, bonobos and orangutans, in sanctuaries and zoos as well as in the wild. Gibbons almost always avoid water; only one case of wading in a zoo was reported. Bipedal wading was reported more frequently than quadrupedal wading for all apes. The fact that apes have the tendency to use a bipedal gait when in water is very interesting and demands further investigation, especially in regard to the development of permanent bipedalism in humans (see unprofitability hypothesis in chapter 6.6). As discussed above (chapter 4.3.3) bipedal wading occurs also regularly in non-hominoid primates and is therefore linked to the general primate anatomy. The use of sticks during wading was repeatedly observed only in orangutans. The only observation of this behaviour in gorillas was published as first description of tool use in wild gorillas. Apes seem not only to use sticks to improve balance, but also to probe the depth of the water.

A special point of discussion is the difference in water contact between bonobos and chimpanzees, and possible behavioural and anatomical adaptations to a swampy environment in bonobos. Kortlandt wrote:

> The slender build, long legs and frequent bipedal gait of Pan paniscus might conceivably evolved as a secondary adaptation to the watery and swampy environment in the deltaic western part of the Zaïrean basin. These features facilitate wading and they reduce the risk of being drowned when sinking through the vegetation mat because a quadruped walker or runner disappears head-first into the mud. Pygmy chimpanzees do indeed occasionally wade in shallow water with a solid bottom (Badrian and Barian 1977). By means of tests in captivity it should be possible to find out whether the species is more willing and better adapted than its relative to cross rivers by wading. Common chimpanzees have occasionally been observed in swamp meadows and forests in the Republic of the Congo, eastern Zaïre and Uganda (Fay 1989 and pers. comm. Kortlandt 1972; Mitani 1992; photo 1). When necessary they jump bipedally like frogs from one tussock to the next. Perhaps the observers of pygmy chimpanzees have not yet ventured into such treacherous habitats. Or possibly the apes themselves are too shy to enter large open swamp meadows. For comparison, orang utans can thrive in Bornean true swamp forests (Galdikas 1978). (Kortlandt 1995, 25)

Later, similar thoughts concerning a functional relationship between long legs and watery environment were expressed by De Waal, who wrote:

> The contrast between the two species may not be absolute (human-reared chimpanzees sometimes learn to like water, and not every bonobo is necessarily attraccted to it), but in general the difference is strinking. It is also understandable. The bonobo's natural environment abounds with rivers and streams, and swamp forests cover a large part of their range. Many areas are seasonally flooded. Although bonobos tend to prefer so-called terra firma forest, they may have been periods in their evolutionary past when water was even more plentiful than it is at present. Both Kano and the Badrians have heard from local people that bonobos catch and eat fish. For many years field-workers found only ape footsteps and holes in the mud of small streams, but no direct evidence of fish catching. On a recent field trip, however, the Badrians saw two female bonobos walking upstream, in the water. They snatched handfuls of floating dead leaves, picking out things to eat. After the apes noticed them and fled, the investigators themselves tried the technique. They disturbed many small fishes hiding beneath the fallen leaves. Susman has observed that the numerous bonobo tracks along streams lack knuckle prints. This suggests to him that bonobos avoid getting their hands wet by assuming bipedal posture when crossing streams.(De Waal 1993, 184)

During this investigation, further rare or unexpected aquatic behaviours were found, like different forms of reactions to rain, different forms of head submersions or washing. Apart from the questionable reports on face washing in gibbons, apes reported to wash their faces or

bodies are commonly animals raised by humans or living in sanctuaries or zoos. However, some examples were also described in the wild. The “rain dance” first described by Jane Goodall was confirmed in other chimpanzee populations, but seems to occur only in this species. Positional behaviour in water seems to be often related to thermoregulation and was also observed in the wild for several ape species. Also playing in water seems to be common, in captivity as well as in the wild, for several ape species.

Drowning in apes is among the best known incidents of water contact in apes, probably because of the tragic component of each such incident. Popular media occasionally interpreted such events as “suicide”, an interpretation which in most cases is more than questionable. All accidents happened in captivity or in released animals. Drowning in wild apes is – for obvious reasons – difficult to be confirmed by direct or indirect observation – a fact which also applies to other mammals. From the descriptions of drowning as well as near drowning, it is remarkable to note that animals that were observed drowning are often described as completely helpless and not able to save themselves even in water within their wading depth. Crandall discussed this point in connection with the drowning of the gorilla Makoko and the near drowning of the orangutan Sandra:

> Makoko had had no opportunity to become conditioned to water, so that the element encountered in his plunge was entirely strange to him. His reactions approximate those of the small orang-utan, Sandra, already noted. He sank from sight almost immediately, apparently making only futile efforts to extricate himself, and was completely submerged when found by the swimming keeper. Certainly he made no effective attempt to swim nor did he seize the steel cables set along the moat side, under water, against such an emergency. (Crandall 1971, 165)

Interestingly, several apes were observed rescuing conspecifics or individuals from other species which were drowning. The fact that one possible case of suicide in one chimpanzee and several cases of killing or attempted killing of conspecifics in orangutans and chimpanzees are described, and on the other hand several apes saved drowning individuals, could be interpreted as indication that apes are aware of the danger of water. Chimpanzee mothers seem to be extremely alert when their young play in the near of water and in the Lion Country Safari Park in West Palm Beach it was observed that mothers slapped their youngs when these approached the moat’s edge (interview with Terry Wolf). Otto Adang, who had several opportunities to observe chimpanzees interacting with water in the Arnhem Zoo, The

Neatherlands, states that “it was very clear that mothers were very attentive with their infants near the moat. [...] They will hold onto them when the infants are near the moat, drinking or play with the water etc., and let go once they remove themselves from the moat. There are also many examples of mothers (or others) retrieving children that venture into the direction of the moat on their own”. However, he had never seen them slap their infants in relation to this (Otto Adang, pers. comm.).

The most interesting example of how a chimpanzee perceived another chimpanzee wading in neck-deep water as an atypical behaviour is exemplified by the chimpanzee ‘Lucy’. She was born in 1964, reared in human homes and started American Sign Language for the Deaf (ASLD) training in October 1970 (Fouts 1997). Lucy was observed on several occasions asking the question “What that” in ASLD when referring to several objects. Roger S. Fouts, who worked with her several years, mentioned an example of Lucy’s use of this sign:

> Most recently she was looking at several photographs of people she knew, and other things. She observed the photographs in a casual fashion except for one which she paid particular attention to and then she asked the experimenter "What that". The photograph happened to be a picture of a chimpanzee wading up to its neck in water. (Fouts 1975, 150)

When asked about the origin of this photograph Fouts answered: “I can only guess about the picture that Lucy was looking at, but it may have come from the chimpanzee island at Lion Country Safari in Florida where certain of the chimpanzees there were noted for not only wading in water, but actually escaping by wading whilst holding on to floating logs” (Roger S. Fouts, pers. comm.) The zoo’s director Terry Wolf confirmed Fouts’ statement and reported on several other interesting behaviours towards water which were observed in this zoo (see this chapter, passim).[63]

Feeding in or at water bodies seems to be common, especially in African apes, where it is observed regularly in bonobos and in western lowland gorillas. In chimpanzees tool use was described to gather algae in water. Drinking behaviour is described in all apes, mostly also in the wild. The present investigation focuses on reports on drinking behaviour in wild or semi-free ranging animals, reporting on captive animals only if other data are scarce. Drinking

[63] It is interesting that these remarkable behaviours were not mentioned in the publications reviewed in the present thesis, although these behaviours (as revealed by the questionnaire) are not unknown to several primatologists, especially to those working in the USA.

behaviour in wild chimpanzees seems to differ between populations. Early reports did not contain many data on drinking, while recent reports contain data even on tool use to drink in wild chimpanzees. In orangutans as well as in chimpanzees, several tool innovations for drinking are described, like sponges or leaves used as cups.

Another interesting behaviour is the drying of the back fur after submersion into water. Sylvia Siddle reported on a female chimpanzee: “She then jumped out of the water rubbing her back on the grass as if to dry herself” (pers. comm.). I repeatedly observed the chimpanzee ‘Cooper’ showing the same behaviour after spending extended periods of time in a swimming pool. This behaviour can also be seen in a captive squirrel monkey (*Saimiri sp.*) drying itself on its back (Anonymous 2010c). Robert Golding, asked about similar behaviours in two gorillas interacting intensively with water in the Ibadan Zoo, Nigeria, wrote: “After being in water, which could be several times a day, especially in the hot dry season, my gorillas had access to an area of grass, although the size of that area steadily reduced as the dry season wore on. Grass grew back and covered a larger area during the rainy season, but I cannot remember the gorillas attempting to dry themselves on coming out of the water, either by rubbing on grass or shaking their bodies, in the rainy season or dry season. They used the water much more during the dry season, one of the benefits appearing to be that it cooled them down which they appeared to enjoy, and they would often remain in the water moat for many minutes. This applies to both gorillas. All the chimpanzees avoided water at all costs and I do not remember a chimp entering the water and thus did not see any subsequent behaviour” (pers. comm.).

Display in water was described in gorillas and in chimpanzees, but not in non-hoiminoid primates. Gorillas and chimpanzees use several objects like trees, branches or ground to produce audible displays by striking them. Chimpanzees might even choose especially suited trees to perform their percussive displays (Smith 1980, 33). Display in water is spectacular and seems to impress conspecifics. Gorillas display in water by splashing (Parnell & Buchanan-Smith 2001a; Parnell & Buchanan-Smith 2001b), while chimpanzees were observed displaying by throwing stones into the water (Nishida 1993, 25).

The inference of data on captive animals on swimming behaviour of wild animals

Data on water use by captive apes is currently being used in a paradoxical way in primatology. The common opinion that apes do not have the anatomical pre-conditions

necessary to develop a swimming ability (see the low-fat hypothesis by Angus, chapter 6.8.1) was strongly influenced by data gathered on captive animals in conditions that were traditionally designed to minimize interactions with water bodies (see chapter 4.3.6). However, primatologists are often unaware of the subtle influence that this data has had on common opinion in this field, so are inclined to neglect data on captive apes kept in settings that allow (and often lead to) a high degree of aquatic interaction.

In the present investigation it was shown that swimming behaviour is highly atypical in apes and still not confirmed in wild individuals. This evaluation can be revised if genetic or observational evidence can be found showing that in some free-ranging ape populations swimming ability occurs regularly. As we saw, in siamangs (*Symphalangus syndactylus*) especially, but also in common chimpanzees and bonobos, there is a theoretical possibility that swimming ability can occur in wild populations. The common opinion that apes are not able to swim in the wild is strongly influenced by data gathered on captive animals in conditions designed to minimalize interactions with water bodies. However, caution should be exercised in this kind of inference.

One striking example of premature conclusions on water use in apes concerns gorillas. As briefly mentioned in the introduction, until the 1990s it was commonly believed that gorillas hesitate to enter shallow water, even when pursued by hunters. Most publications mentioning gorillas' reluctance to enter water quote George Schaller. However, Schaller's statement was based mainly on the lack of observations of gorillas interacting with water and on a single observation by Charles Cordier (Charles Cordier, pers. comm. to Schaller 1963, 298). Although Schaller stuck to the known facts at this time, the general readiness to accept this sparse data as conclusive was influenced by the behaviour of gorillas in captivity. As we saw, zoos traditionally are designed to minimize or completely prevent an interaction of apes with deep water. However, gorillas' interaction with water in captivity was much more variable than suggested in the succinct statements on gorillas' water use in the past. Already by the end of the 1870s, the second living gorilla exported to Europe was described as very fond of playing in water (Falkenstein 1879, 153), and four decades later a captive gorilla was described as enjoying bathing in warm water (Cunningham 1921). Particularly insightful is the statement by Clarence C. Carpenter when describing the behaviour of two captive mountain gorillas which had access to a pool large enough for the animals to bathe: "Their response to water was always positive for purpose of drinking, playing and bathing"

(Carpenter 1937, 112). The same author also maintained that a regular access to water bodies "is one of the important factors in the success of the San Diego Zoological Gardens in keeping these animals in captivity healthy, contented and growing normally" (Carpenter 1937, 112). Robert and Ada Yerkes, after revising the early literature on water use by gorillas, had already noted a certain contradiction between the common opinion of wild gorillas being afraid of water and the reports on captive gorillas playing in water or bathing (Yerkes & Yerkes 1945, 409). In the 1970s and 1980s, reports on captive gorillas clearly showed that gorillas do not have an instinctive fear of water, and water can be used as a tool for enriching the environment (Brown et al. 1982; Cousins 1978; Golding 1972; Quick 1976). However, this data did not change the general negative views on water use by wild gorillas.

Interestingly, some early and widely ignored publications reported wild gorillas definitively as not being afraid to enter water. In the expedition of 1929-30 for the study of mountain gorillas (*Gorilla beringei beringei*) in the Albert National Park, Belgian Congo (today the Democratic Republic of the Congo or DRC), Harold C. Bingham found evidence of gorillas wading through a swollen mountain stream:

> At the place of fording there was a moderate current. The water was not deep enough to require swimming, but it was necessary for the observer to make use of submerged rocks to keep boot tops above water. The outstanding evidence of this crossing was the slippery banks up which the dripping animals had scrambled. (Bingham 1932, 60)

A further observation of wild gorillas interacting with water was published four decades later. In East Africa, mountain gorillas of Kahuzi-Biega in Zaire (today the DRC) were observed wading in 60 cm deep water (Casimir 1975). In 1981, Herman A. Regusters observed and photographed lowland gorillas in swampy forests in the north of the Republic of the Congo (Regusters 1983), at a time in which "it was thought that the gorilla did not exist west of the Congo River, based on presumed fear of water" (Regusters & Vandusen 1985, 176). Some years later Colin P. Groves and J. Sabater Pi described two western lowland gorillas' (*Gorilla gorilla gorilla*) nests "on a very large trunk at the very edge of a river bank - an anomaly considering that gorillas are supposed to be much afraid of water" (Groves & Sabater Pi 1985, 29). In the same paper, the authors write that "Fang guides maintained to J.S.P. [J. Sabater Pi] that they have many times seen gorillas bathing in forest streams". Until the end of 1980s, these reports were ignored or regarded as showing an exceptional behaviour in gorillas. The decisive turnaround concerning the general belief that wild gorillas avoid entering water at all

times came with the publications on western lowland gorillas feeding on aquatic plants, wading or displaying in water of streams and swampy areas from the late 1980s onwards (Doran-Sheehy et al. 2004; Magliocca & Gautier-Hion 2002; Nishihara 1995; Parnell & Buchanan-Smith 2001b; Williamson et al. 1988).

An interesting example (briefly presented in chapter 4.3.3) of wild apes showing a completely unexpected degree of interaction with water concerns observations of savannah chimpanzees (*Pan troglodytes verus*) at Fongoli, in Senegal (Pruetz & Bertolani 2009). Several male, female and juvenile chimpanzees were regularly observed in ponds temporary filled with rain water in the beginning of the rainy season or in the riverbed of a small stream (Jill Pruetz, pers. comm.). The chimpanzees stay for 30 - 45 minutes in the water, where they rest, groom and play (Pruetz & Bertolani 2009); (Paco Bertolani, pers. comm.). This behaviour is documented by video footage whereby six adult chimpanzees enter carefully into a pool (Sakoto pool) created by recent rainfall. They sit immersed up to their chests, holding onto the vines for safety, although the pool is evidently not deep (Roach & Lanting 2008). This behaviour is radically opposite to the widely held belief that common chimpanzees are highly aquaphobic animals at all times.

Similar observation can be done in non-hominoid primate species. Spider monkeys can be usually kept on islands surrounded by deep water moats (Crandall 1971, 97), and specialists often state that they never observed these species swimming. These two facts suggest that these animals are not able to swim. However, indirect and direct evidence prove the swimming ability of spider monkeys. A report suggests that a female spider monkey crossed by swimming between Barro Colorado Island, Panama, and nearby islands (Campbell 2000; Mutschler *et al.* 1998); (Christina Campbell, pers. comm.). Another publication suggests that an adult male and female spider monkey swam to the Orchid Island, a small forested island close to Barro Colorado Island. However, the authors could not exclude the theoretical possibility that these animals (as former unwanted pet monkeys) were released there, although both individuals were evidently not tame (Milton & Hopkins 2006). Clear evidence came from captive animals. A female white-cheeked spider monkey (*Ateles marginatus*) escaped sporadically from an island by swimming over a water moat in a zoo in the Parque Barigui, (near Curitiba, in Brazil), and was found in the mainland in the next morning completely wet (Tereza C.C. Margarido, pers. comm.). At Orana Park, a wild-life sanctuary in Christchurch, New Zealand some of the spider monkeys escaped by crossing the moat surrounding their

islands (Christina Campbell, pers. comm.). Crandall reported on a group of spider monkeys escaping from an island by wading, “one after another, each nearly upright and with one hand clutching the upraised tail near its tip” (Crandall 1971, 98). Recently, data were published on wild spider (*Ateles geoffroyi*) and howler (*Alouatta pigra*) monkeys crossing sporadically a large Mesoamerican river (Chaves & Stoner 2010; on swimming howling monkeys see also Neville *et al.* 1988). Carpenter reported on howler monkeys escaping from islands by swimming. According to Central America natives, these animals swim "mismo un hombre" (like a man), demonstrating an overhand stroke (Carpenter 1934, 33). This example shows that the combination of data “primate highly reluctant to enter water in captivity” and “absence of reports on swimming behaviour in captivity and in the wild” should not been taken as a guaranty that this species is unable to swim.

For similar reasons it is well possible that wild apes under favourable and exceptional conditions could be able to cross deep water barriers by swimming. Although large rivers undoubtedly present barriers in the distribution of gibbons (Geissmann 1991), orangutans (Goossens *et al.* 2010), gorillas (Anthony *et al.* 2007; Schaller 1963), bonobos (Eriksson *et al.* 2004; Kano 1992, 59) and common chimpanzees (Gonder et al. 2006; Gonder 2000), the same is true for terrestrial fauna including species known to be able to swim (Ayres & Clutton-Brock 1992; Gonder et al. 2006) or to fly (Hayes & Sewlal 2004). Additionally, although an early hypothesis (Schwarz 1934) stating that large rivers can form barriers for chimpanzee gene flow was confirmed, the same investigation revealed that at least one river (Sanaga River in Cameroon) does not represent a complete barrier (Gonder 2000). Kathy Gonder further wrote: “The Sanaga is small – I’ve no doubt chimps can/could get across it if they wanted to. Certainly they cross on occasion – we do detect migrants. Also, the Sanaga River delimits the distributions of several pairs of primate species and subspecies (e.g., drills and mandrills). It’s also a well-known boundary for many different kinds of animals with differing ecologies and certainly different swimming abilities. There are also many more animals whose distributions are not affected at all by the Sanaga” (Kathy Gonder, pers. comm.). One possibility to explain these contradicting results is that slow flowing and strongly meandering rivers might change their positions over time and so switching land masses from one side of the river to the other (Eriksson *et al.* 2004). However, instead of considering data on migrant apes as unreliable or insignificant, or explaining it through crossing rivers by other ways than swimming, the

present results show that the possibility of crossing by swimming should be considered as an alternative explanation.

The less frequent and less intensive interaction with water by apes compared with humans has to be discussed in more detail. Most zoos or sanctuaries do not offer conditions favourable to the development of safe aquatic interactions in apes. The conditions in ape enclosures (steep and slippery water moats without vegetation, with electric fences) fulfil several relevant aspects concerning aesthetics, safety (for the visitors) and low costs. By using water as barriers, the interaction of apes with the moats is undesirable simply because an accustomed to interact with water has more opportunities to cross the water moat. Although rarely stated, most zoo directors would prefer the risk of a drowned ape than an ape whom escaped from its enclosure and possibly attacked the public.

In sanctuaries and zoos offering a safe access to water, many individuals from all great ape species show an astonishing variety of interactions with water. Additionally, the present investigation revealed that several species of apes showed interesting behaviours and innovations regarding aquatic activities in the wild. It is indisputable that environmental settings influence in many sensible ways apes' interaction with water. It can be inferred intuitively that apes and humans, for instance, usually avoid bodily contact with cold water, and that it may be expected that apes having the opportunity to interact with water in a tropical climate will show a greater degree of direct contact with water than captive apes living in zoos in temperate zones. However, in most cases it is difficult to identify precisely which behavioural features are influenced by which environmental factors.

One important factor for the development of behavioural patterns related to water use might be a low level of aggressiveness in the group. Some zoos and research centres, with a large number of animals kept in a relatively restricted area with a high level of food competition do not fulfil these conditions. In cases where animals were released into a new group with access to deep water but without a phase of habituation, it happened that the animals accidentally fell or jumped into the water to escape an aggressor. In these situations they often died (Angus 1971; Cousins 1978; Crandall 1971), or had to be rescued by humans (Jon C. Coe, pers. comm. in (Goodall 1993)) or, exceptionally, by other apes (Anonymous 2000; Fouts & Fouts 1993; Mottershead 1960). Jon Coe, who worked on the design of the chimpanzee exhibit in

the Detroit Zoo, wrote about the cause of the accident with the chimpanzee 'Jo Jo', rescued by a human (see chapter 4.3.3):

> The famous rescue by the truck driver was at the project our firm designed. The immediate cause was bad management, in my opinion. We specifically designed the entire project to have two separate exhibit and holding areas for the eventuality that the troop would someday split or at least some individuals would be incompatible. This troop was made up of newly introduced apes. The dominant male severely attacked the victim, biting off several fingers and leaving other cuts and injuries. Rather than separating the victim or forming a second group in the second area or rotating with the first group, the director ordered staff to send the victim back out with the same troop only a day or two after the fight as I recall. When the victim saw the alpha male charge after him again he chose to leap into the moat, perhaps hoping to leap across and escape, rather than face a second attack. The other drowning occurred some weeks earlier from memory. This was on opening day or the second day after opening. A mature female calmingly exploring the new exhibit came to a point where the moat looked most narrow and decided to see if she could leap across. She couldn't and unfortunately drowned. She was the first fatality there. (Jon Coe, pers. comm.)

He compared the two accidents:

> The two occurrences were as different as could be. The first was a calm and considered leap, the second a panic reaction of escape at any cost in my opinion. The moat in question was a 'v' shaped clay-lined trench cut through the earth 5' (1,5m) deep by 20' (6m) wide. This configuration was selected because it was low cost compared to concrete construction and the resulting cost savings enabled the zoo to provide the chimps with a far larger area (about ¾ acre or 1335 m2). The clay lining caused the water to stay muddy for many months. This made it difficult to locate the chimps when they were underwater. Dr. Frans DeVaal was our advisor and supported this design. He had worked with chimps with water moats at Bergers Zoo in Holland and wanted them to have as much space as possible. (Jon Coe, pers. comm.)

In hind sight, he believed that one possible problem was that the deepest part was in the centre of the moat. He wrote:

> Other concrete lined water moats were sloped more gradually with the deepest water at the point furthest from the chimp shoreline. A second possible problem was that in perspective, 6m doesn't seem very far to jump. We had planned to provide extensive reedbed shallows on the chimp side of the moat to extend the distance and I think this was successful where it was applied. But the area had many fine large oak trees we wanted to save and in order to

> minimize root cutting much of the length of the shoreline was steep. It was at these narrowest points the chimps jumped. As I recall during our design discussions our greatest concern was young chimps falling into the water during play. We really didn't discuss the possibility of chimps intentionally leaping into the water. (Jon Coe, pers. comm.)

He concluded that "pools are better as enrichment features than as barriers if and when the apes are taught/conditioned to play safely in the water" (Jon Coe, pers. comm.). One positive example is the Arnhem Zoo where a method to monitor and facilitate habituation to water of chimpanzees with no previous experience with deep-water moats was developed (van Hooff 1973). In the Lion Country Safari Zoo in West Palm Beach, Florida, after some drowning accidents, single chimpanzees were consequently isolated as soon as it was observed that they had problems with the rest of the group, and later reintegrated in the group. This preventive measure reduced the accidents in water (interview with Terry Wolf).

Especially positive for an intensive interaction with water seem to be natural or semi-natural water bodies, characterized by a gentle slope and the absence of sharp edges or slippery ground – see, e.g., Mottershead (1960, 20) –, giving the animals the opportunity to secure themselves on shore plants or on rocks, vines or similar structures when exploring the water. One example of such an exhibition can be found in the Lion Country Safari Zoo. From his experiences with chimpanzees constrained by a water moat at Chester Zoo, Mottershead concluded:

> I have now come to the conclusion that it is quite safe to confine Chimpanzees by barrier of water, providing that the water is at least 15 feet in width and not less than 4 or 5 feet deep. It is of course a great advantage if the surrounding area used by the public is slightly higher than the islands where the Chimpanzees are, but if this is impossible I would suggest widening the water barrier. To my mind, the water bed should slope to the bank, so that if a Chimpanzee falls into the water, it is able to walk out. A waterway constructed of clay, etc., is far more advisable than one constructed of concrete, as in my opinion a concrete pool which is the same depth all round would prove to be rather dangerous. It is possible that a Chimpanzee might accidentally fall into the water and drown since it is very questionable as to whether it would swim. (Mottershead 1960, 19-20)

However, favourable conditions are uncommon in most zoos (Brown et al. 1982; but see Golding 1972; Maple & Hoff 1982). Several zoos have only a deep-water moat or moats containing only a very narrow part with shallow water. Often animals do not have free access

to deep-water bodies,[64] since these are mostly secured with electric fences or other barriers; see, e.g., Mottershead (1960).

The results of the present chapter show that the topic aquatic activities of apes is more complex than usually assumed, and it underlines the need to consider all available data on wild and captive animals to predict a species' potential interactions with a broad range of environmental settings in the wild.

4.4 Swimming in apes

The swimming behaviour of the chimpanzee 'Cooper' and the orangutan 'Suryia' is described in detail here. These animals were filmed[65] and their owners were interviewed. The results of this observational investigation were published in (Bender & Bender 2013). Parts of the publication are reported here. Ethical clearance was obtained from the Animal Ethics Screening Committee of the Witwatersrand University.

4.4.1 Methods

Description of animals

Cooper is a cross-fostered male common chimpanzee (*Pan troglodytes*) born in 2003. He was raised from the age of 2.5 years in a human environment by Jill and Brad James in Malden, MO. According to the owners, Cooper's approximate body weight was 36 kg in August 2010. At 4 years of age in playful interactions with the owners, Cooper began to submerge his head, first in a bath tub and later in the shallow part of the swimming pool. Without previous knowledge of the fact that apes are susceptible to drowning, the owners allowed Cooper to play in the shallow part of a backyard swimming pool, where he continued to submerge regularly. The presented evidence is based on our own observations, our own video footage, video footage by the owners, and interviews with Cooper's owners.

Suryia is a cross-fostered male orangutan (*Pongo pygmaeus*) born in 2003. He was kept in T.I.G.E.R.S. (The Institute for Greatly Endangered and Rare Species), a private zoo in Myrtle Beach, SC. During our investigation in August 2010, Suryia's body weight was

[64] Following the recommendations of the Association of Zoos and Aquariums (Ross & McNary 2009), several zoos are being redesigned without deep water moats as barriers, especially for chimpanzees. The AZA recommends using water as enrichment in the form of small streams or water jets, and to limit water bodies in chimpanzee exhibits to a depth of <0.6m.

[65] All videos mentioned in this chapter are displayed here: http://onlinelibrary.wiley.com/doi/10.1002/ajpa.22338/suppinfo

approximately 38 kg (Bhagavan Antle, pers. comm.). At the age of 7 months, Suryia was daily bathed (B. Antle, pers. comm.). At the age of 3 years, as part of weekly enrichment activities during the summer months, Suryia was regularly exposed to the shallow and deep parts of a pool, initially wearing a life jacket. Suryia was specifically trained to swim and to dive. The presented evidence is based on our own observations and our own video footage, interviews with Suryia's owner Bhagavan Antle and with Robert Johnson (animal trainer at T.I.G.E.R.S.), and Antle's video footage.

Data collection

We observed the chimpanzee Cooper, during two different periods: from August 9, 2010 to August 12, 2010 (3 sampling days, approx. air/water temperature 35/34°C) and from August 9, 2011 to August 11, 2011 (3 sampling days, approx. air/water temperature 29/28 °C), in total c. 24 observation hours. The pool dimensions were 12.10 m 3 5.5 m, the depth was 0.88 m sloping to 2 m. Cooper could stand bipedally in the shallow part of the pool, with water at chest or chin level. He was not able to stand in the deep part of the pool. Videos 3 and 4 were made in the deep part of the pool; video 5 was made when Cooper swam from the shallow to the deep part of the pool.

We observed the orangutan Suryia, from August 14, 2010 to August 17, 2010 (c. 16 observation hours). The pool dimensions were 15 m 3 10 m, sloping from 0 m to a maximal depth of 2.5 m (approx. air/water temperature 30/32°C). The videotape of Suryia swimming (video 6) was made by the owners in the deep part of the pool.

Both animals were observed using an ad libitum sampling strategy and by continuous recording while the apes were freely interacting with water in swimming pools. We used analog and digital cameras and video cameras both on land and under water. I was in the swimming pools, taking close-up photos and videos from above and under water. My assistant Nicole Bender was based on the edge of the pools, taking videos from the land.

It is important to note that the quality of video footage used here cannot be compared with common experimental studies (e.g., using high-speed film analysis for kinematic studies as applied under laboratory conditions, or using trained animals which performed the studied movements under ideal conditions and on command). For example, the chimpanzee Cooper swims only in unfavourable conditions for filming (in a private backyard swimming pool). Since Cooper was not trained to swim or to show swimming behaviour on command, this

behaviour is displayed only sporadically and during unpredictable playing bouts. Given his unpredictable behaviour towards strangers, the use of multiple assistants to record his aquatic behaviour from different angles was not possible.

4.4.2 Results

Swimming and diving behaviour in the common chimpanzee 'Cooper'

During the first observation period (August 2010), Cooper was not able to swim. Cooper could not wade quadrupedally in the shallow part of the pool — he had to stand bipedally to keep his head above the water (video 1). The most conspicuous behavioural patterns were Cooper's almost compulsive tendency to submerge (videos 2 and 3) and the high degree of acquaintance with water. We confirmed the observation by Jill James (pers. comm.) that, under water, Cooper always covered his eyes and nose with the left hand (sometimes with both hands). He was, therefore, not able to use visual orientation during submersions. When fully submerged he showed a great variety of positional and play behaviours: sitting or lying in prone, supine or lateral positions on the floor of the pool (video 2). Under water, he frequently used the tactile sense of his right hand and feet to reach for objects or humans. The longest submersion that we videotaped was of 15 s.

During the first investigation period, for safety purposes two ropes were stretched at the water surface from one side of the swimming pool to the other in the deep part of the pool. Cooper began immediately to explore the ropes and within a few minutes after the first contact with them he began to display a broad variety of new aquatic activities. For example, the day after the ropes were installed he repeatedly made full submersions in deep water holding on to one or two ropes, often trying to grasp (blindly) with one foot or one hand objects placed 2 m deep on the floor of the pool (video 3).

In the first period of observation, some behavioural patterns indicated that Cooper would be able to develop the ability to swim at the water surface. For example, on one occasion after completely submerging in the deep part of the swimming pool in an erect position, Cooper released the ropes for the first time in what seemed to be an explorative behaviour (unassisted, full submersion in deep water). To emerge, he vigorously kicked with the legs—both simultaneously and alternately (video 4). However, it is difficult to establish the actual propulsive character of these movements (videos 4 and 5). Although these videos do not fully

allow a fine-grained description of the swimming pattern, the direct observation of this behaviour suggests that the movement is similarly structured as the human breaststroke kick.

Between the two observation periods (on August 25, 2010), Cooper was observed by his owners “treading in the deep end” of the swimming pool (Jill James, pers. commu.). Over subsequent days the owners observed and filmed Cooper on several occasions swimming approximately 2–3 m from the shallow part of the pool to a rope stretched across the deep part of the pool (video 5). He moved his hands alternately backwards and forwards, but more laterally than in the typical doggy paddle of other primates. The feet were moved mostly simultaneously in a breaststroke-like pattern, in which the feet are dorsi-flexed at the end of the recovery phase and at the beginning of the out-sweep. At this moment, the feet were rotated outwards at the ankles, resembling the leg patterns of human breaststroke swimmers. Propulsion was generated when the feet were moved in a semicircular movement outwards and backwards. During swimming, he always kept his head above water (Fig. 4.4). The second period of investigation was planned to observe and videotape Cooper swimming. However, during this period he did not exhibit any swimming behaviour.

An interesting incident occurred in the second period of investigation. When I prepared scuba diving gear for underwater footage, Cooper got highly interested in the air streaming out of the regulator. He placed the regulator in his mouth, began to breathe vigorously through it first out of the water, and within few minutes, partially under water. As Cooper always submerged covering the eyes with one or both hands, I closed Cooper’s eyes with his hand, in an attempt to signal that he could submerge while breathing through the regulator. Afterwards Cooper began to submerge completely, first breathing very fast and superficially, and later more calmly. After some minutes, he was able to hold the regulator in the right position. Subsequently, Cooper dived breathing through the regulator, extensively exploring this new form of underwater activity. During the 47 minutes and 53 seconds of videotaped time, he spent 31 minutes and 40 seconds in total under water in 59 different submersion bouts, with a mean submersion time of 32 seconds per bout. The longest dive was of 2 minutes and 40 seconds. He only stopped after the air was completely consumed. Cooper did not repeat scuba diving over the subsequent days.

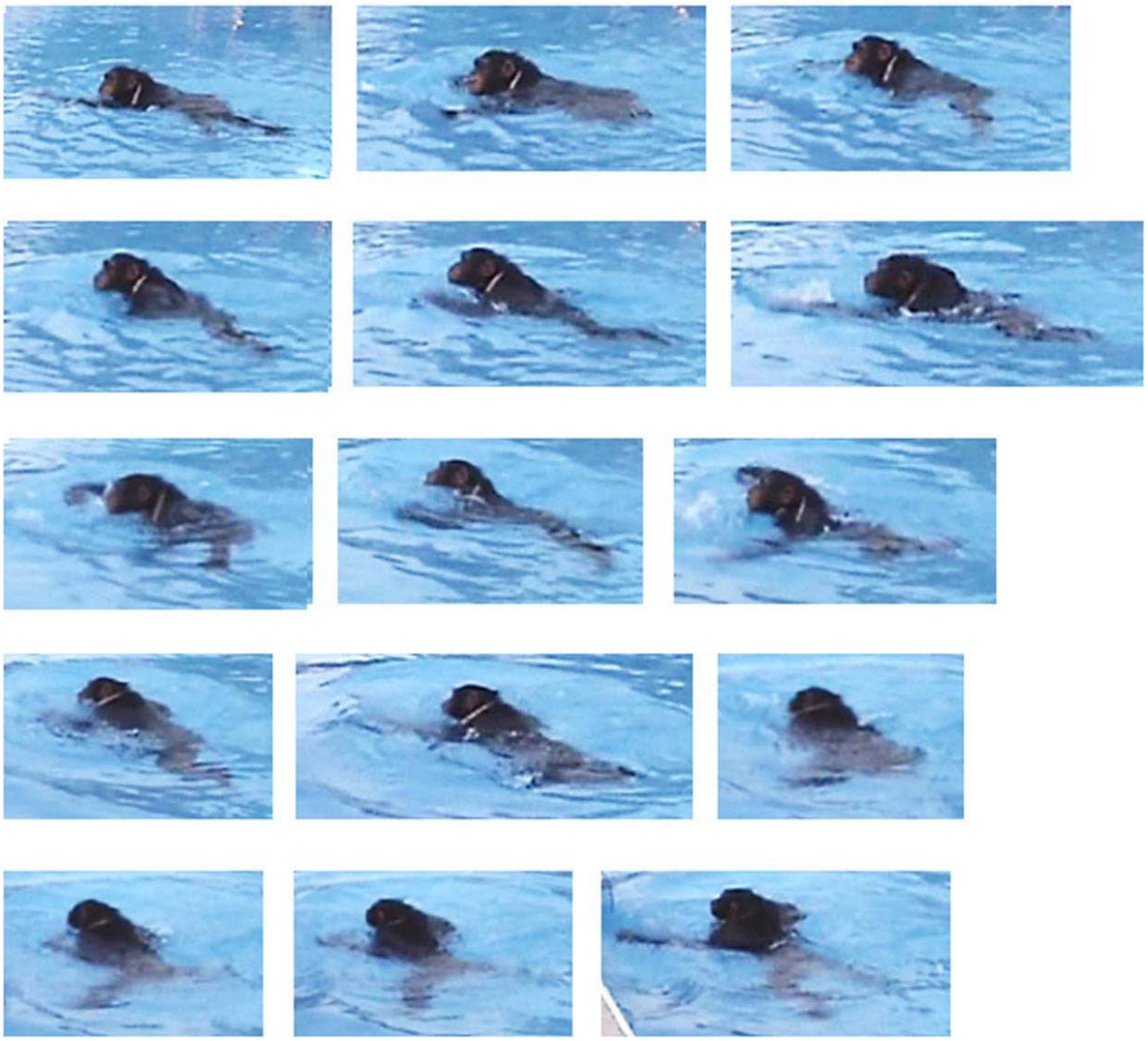


Figure 4.4 Cooper swimming. The alternate arm stroke slightly deviates from the typical doggy paddle of other primates by more lateral components. The simultaneous action of the legs (especially shown in the last three pictures) is atypical in terrestrial mammals. The propulsive movements improve the buoyancy to such an extent that head and shoulders are clearly out of the water.

Swimming and diving behaviour in the orangutan 'Suryia'

At the age of 7 years (in June 2010, 2 months before this investigation) Suryia began to swim under water over short distances from one keeper to the other. During our observations in August 2010 he was able to fully submerge and swim unassisted under water over a distance of c. 2–4 m. He moved his hands alternately forwards and backwards, with more lateral components than the typical doggy paddle of other primates. The main propulsion was caused by the actions of the feet moving alternately in a pattern similar to that used in human breaststroke. However, Suryia's leg action technique diverged from the human breaststroke

kick in at least two ways: he was able to bring his feet close to or even in front of his hips in the recovery phase of his breaststroke kick; and he showed a higher degree of abduction in the recovery and propulsive phases (Fig. 4.5 and video 6).

Suryia was able to open his eyes under water and swam at the water surface with the face immersed. As Suryia could see under water, he grasped for objects at the bottom of shallow water. In the following months after our investigation, Suryia improved his swimming and diving skills. He began to swim from the shallow part to the deep part of the pool over a distance of c. 6 m, displaying a more coordinated and efficient swimming pattern (video 6). In the first months of 2012, Suryia began for the first time to swim holding the head above the water. According to Robert Johnson (pers. comm.), Suryia is currently able to swim about 12 m.

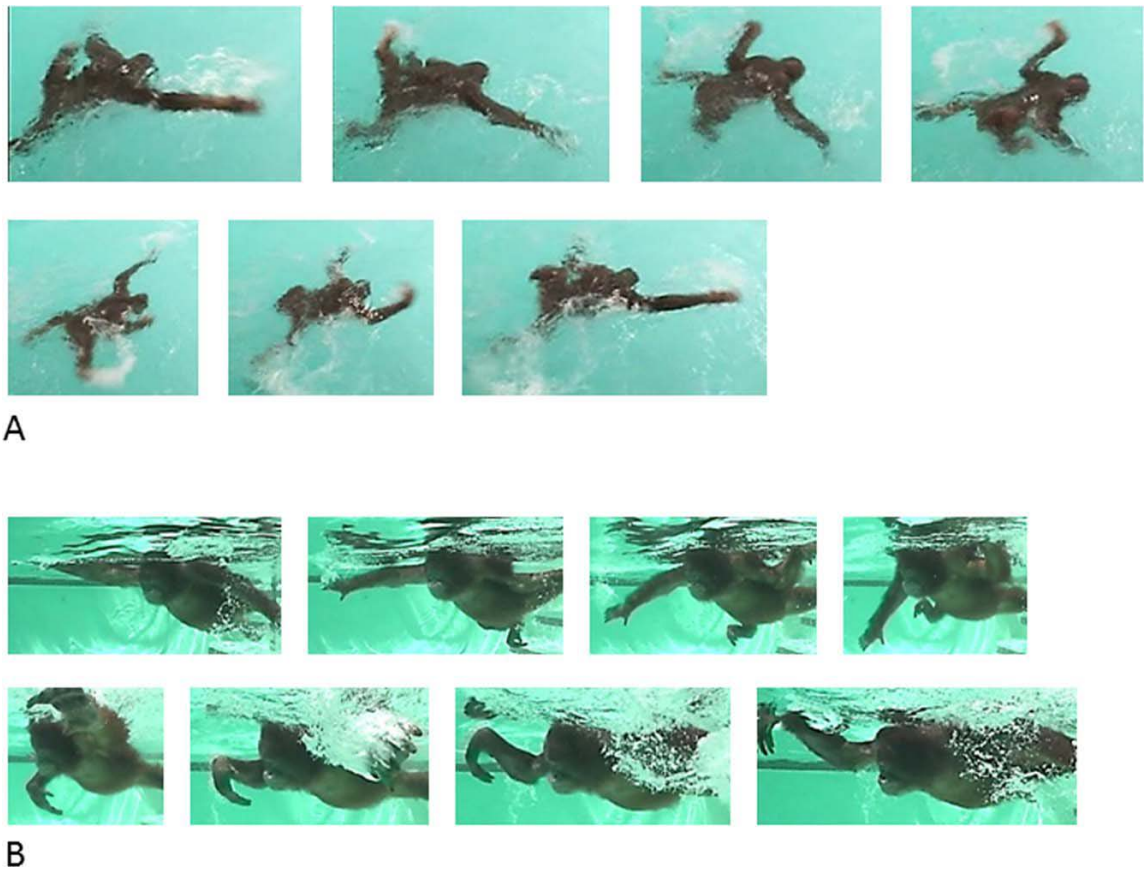


Figure 4.5 (a): Suryia swimming, view from above. The most characteristic elements are the high range of limb movements, especially from the hind limbs, and the lateral component of hind and front limbs. See also video 6 for the atypical use of hind limbs in an alternate breaststroke kick. (b): Suryia swimming, view from the side. The action of the hands and feet during the stroke is shown. Suryia keeps his eyes open under water. See also video 6, where Suryia swims with the head out of the water.

4.4.3. Discussion: the role of learning in the development of swimming behaviour and of fear of water

As described in the review on human aquatic activities (chapter 5), learning to swim occurs often at an early age in humans and can occur by imitation or by active teaching. Teaching new skills by mothers does not only occur in humans, but also in wild chimpanzees, as Boesch observed in chimpanzees opening nuts with stones in the Tai forest. A part from stimulating and facilitating the infants to open nuts by providing them with tools and nuts, two mothers were observed to actively teach their infants which had difficulty to open their nuts. One mother demonstrated the right position of the nut and the other showed the proper grip of the stone used as hammer (Boesch 1991). Interestingly, semi-aquatic animals which swim instinctively, as for instance the European river otter, also have a phase of learning to improve swimming abilities. While otter mothers impede their cubs to enter water when they are not yet mature (Wayre 1977, 24), the mothers actively encourage swimming in their cubs when they regard them as ready to do so (Miles 1989, 77). In American river otters it was observed that mothers dragged their cubs into the water by grabbing them at the scruff (Liers 1951).

Learning by imitation is common in humans and in apes (Gibson & Box 1999, 327-331). The reviews in chapter 4 indicate that the degree and variety of aquatic interactions in apes has a cultural aspect – certain behavioural traits are found more frequently among certain ape populations, as in the case of the chimpanzees at Fongoli. The apes described as able to swim in previous chapters learned to do so in different environmental contexts and through different degrees of contact with humans. It could be argued that these behaviours developed by imitating swimming humans. This is, in fact, the most common assumption expressed by non-primatologists (and occasionally also by primatologists who answered the questionnaires on primates' interaction with water) when confronted with the data on swimming apes. However, this assumption is highly improbable, as the cases of the chimpanzees Bilinga, Shasa and Barbara clearly demonstrate. Bilinga was kept on an island in a semi free-ranging setting, where he did not have the opportunity to observe humans swimming. His swimming behaviour developed in the attempt to reach a boat carrying food, and was, therefore, highly related to a direct reward. Instead of assuming that Bilinga learned to swim by imitation, it is more probable to assume that this specific behaviour developed in a place where chimpanzees were allowed to interact regularly with water. In fact, feeding sessions occurred in water

(Yann Le Hellaye, pers. comm.), and chimpanzees on the islands became more acquainted with water, as it would be expected in wild chimpanzees. Bilinga's swimming behaviour is only one (although an unusual one) among several interesting behavioural traits related to water in the chimpanzees of the rehabilitation programme H.E.L.P. Congo.

Unfortunately, nothing is known about the conditions in which the chimpanzee Shasa was kept before she came to the sanctuary J.A.C.K. Her behaviour is highly interesting, as she was very young when she escaped from the island where she lived in the sanctuary. It can only be speculated about a possible influence by humans on her swimming behaviour. The chimpanzee Barbara (who crossed a 6 m wide water moat underwater in the Lion Country Safari Zoo in Florida), also did not have the opportunity to observe humans swimming under water. Her diving abilities probably developed through the combination of a favourable environmental setting and the prospect of a highly prized reward (she escaped several times to beg for beer in the zoo's restaurant (interview with Terry Wolf on 19 August 2010)). On hot days, several chimpanzees of the Lion Country Safari often enter the water to sit chest-deep in water in niches close to the shore. This is possible because in this zoo chimpanzees have free access to the water, as no electric fences are installed at the edge or inside the moats. The chimpanzees usually hold onto the vegetation growing in and at the water's edge to enter, stay and then leave the canal. In the case of Barbara, this behaviour led to a high degree of acquaintance with water. It can only be speculated on the specific steps undertaken by Barbara when she began to submerge, as this initial phase was not observed. The zoo director, Terry Wolf suggested that Barbara might have learned to dive after submerging accidentally and pulling on the underwater vegetation to come out of the water (interview with Terry Wolf on 19 August, 2010). Another possibility is that Barbara began to submerge as an explorative, playful behaviour.

The natural conditions in the Lion Country Safari Zoo led other chimpanzees to a high degree of acquaintance with water. For instance in 1985 or 1986, Bashful, an adult male common chimpanzee, discovered what can perhaps be regarded as one of the most unusual tool-uses for apes: using a log (1.20 m x 0.15 m) or other floating objects under his armpit as a buoy, he repeatedly crossed a 15 m wide moat to visit chimpanzees on another island. The canal was originally made deep enough to deter crossing by wading (about 2.4 m). However, the machine used to dig out the canal had apparently left a shallower ridge (about 1.8 m) on the moat floor. With the help of the log, Bashful was able to feel this ridge with his feet while

crossing the canal in a bipedal position, sometimes losing balance and bouncing in the deeper water with his head going under. Bashful stopped crossing the canal after he got entangled once in aquatic plants and reached the island exhausted only after a long struggle (interview with Terry Wolf on 19 August, 2010).

A different situation concerns Suryia and Cooper. The orangutan Suryia was systematically exposed to water at an early age as part of an enrichment programme in close interaction with humans, in which a life jacket was initially used to allow a safe interaction with deep-water bodies. In this programme Suryia was often encouraged to submerge and to swim under water. However, the "swimming technique" he gradually developed was probably neither acquired through imitation nor as a result of inputs given to him to shape a specific movement pattern. Suryia developed a highly unique swimming pattern in an attempt to use his limbs for propulsion in water for short distances.

Cooper developed his swimming behaviours in close interaction with humans, but imitation can most probably be excluded as an important part of the development of this behaviour. Although Cooper already had the opportunity at a young age to see humans swimming in the backyard pool, he never showed any attempt to swim before being given the opportunity to dive at the ropes in the deep end in 2010. A precondition for the development of swimming skills was the ability to submerge, a behavioural pattern developed through imitation (see chapter 4.4.2). But as in Suryia, Cooper developed the specific swimming ability by trying different limb movements; the resulting "swimming technique" has both similarities and differences compared to Suryia's movements through water.

Besides the interaction with humans, Cooper's degree of acquaintance with water is also the product of his personality. Cooper has a strong sense of curiosity and is constantly searching for unusual interactions with his immediate environment. With regular access to a swimming pool, water became an important extension of his environment and a place where he could extensively interact with humans, play and use the water for thermoregulatory purposes. However, unlike the chimpanzees Bilinga, Barbara and Shasa, who tried to reach a certain place which was only accessible by crossing a deep-water body, Cooper's swimming abilities did not emerge in connection with a specific reward, but as one of several play behaviours related to water.

A possible common aspect of chimpanzees' habituation to water is that cross-fostered individuals are often bathed and have therefore a stronger contact with water than wild chimpanzees (see exception in chapter 4.3.6 on wild chimpanzees interacting with water at Fongoli, Senegal). However, it is certainly wrong to assume that all young apes which are regularly bathed will later develop a strong acquaintance with water. Probably all hand-raised apes are bathed regularly, as their body odour is often perceived as unpleasant by humans and they usually have to wear a nappy when kept in human houses. It is probably intuitively perceived by laymen that mere bathing automatically leads to overcome apprehension towards water or even to the development of swimming ability. For instance, an author wrote an article about the hand-raised female chimpanzee, Eva. Since Eva was not regularly bathed as an infant, he expressed the possibility that this contributed to Eva's reluctance to interact with water, as she regarded water as something completely unusual (Schneider 1950, 547-548). However, data from the above presented review (see chapter 4.3) contradict this assumption. Several apes that were regularly bathed at an early age enjoyed splashing water when it was possible to them to stay outside of the water, but behaved often very carefully towards deep water-bodies. In fact, in a shallow tub it is not possible to experience the three dimensionality of a large body of water. Therefore, Eva, who was also described as enjoying the play with water (Schneider 1950, 547), showed a usual reaction for a chimpanzee.

The situation is different when human infants are not only bathed, but specifically habituated to water in domestic bath tubs. In the preliminary stages of swimming lessons, parents are often advised on how to get their children used to water during bathing. This technique is often suggested by modern swimming instructors (Bauermeister 1984; Bresges 1973; Kennel 1978; Mönkemeyer 1988; Prudden 1974; Timmermans 1975). Such a programme will not lead directly to swimming ability, but will teach a child to submerge its head under water – an important pre-condition for swimming in very young humans (own observation). Although not planned as a systematic training programme, the playful behaviour between humans and the chimpanzee Cooper in a tub and later in a swimming pool can be regarded as a similar process. Cooper did not learn to swim through this interaction, but he learned to submerge his head, which allowed him to develop a degree of interaction with water which was – to our knowledge – not observed in any other chimpanzee to date.

In the wild, local differences in aquatic activities within the same ape species might indicate that aquatic behaviours depend equally on learning processes. While the mountain gorillas of

Mt. Kahuzi show several aquatic behaviours like crossing creeks, sitting in water and feeding in water (Casimir 1975), other populations in the Virunga Volcanoes were described as very reluctant to enter water (Schaller 1963, 29, 298-299). Large individual differences in attitudes towards water were also described among chimpanzees of the same unit-group (Nishida 1980). In opposition to humans and apes, learning by imitation is debated in non-hominoid primates. Visalberghi and Fragaszy point out that if a novel behaviour spreads in a primate group, such as tail dipping for drinking purposes in captive hamadryas baboons, it has to be discussed if this happens due to imitation or to similar environmental circumstances leading to independent innovations by several individuals (Visalberghi & Fragaszy 1990b, 255-257).

There is evidence that local cultural transmission occurs both in captive as well as in wild apes (Dindo et al. 2011). However, cultural transmission concerning water use in captive apes is probably influenced by factors which rarely or never occur in the wild. Wild apes learn survival competencies in interaction with natural environments (Whiten *et al.* 2009). This interaction is characterized by a high degree of phenotypic plasticity (Van Schaik et al. 2010), i.e., flexible responses of the same genotype to varying environments (West-Eberhard 2003). As mentioned above, there is evidence that geographic variations concerning water use occur in apes, for example in orangutans (Van Schaik *et al.* 2010), chimpanzees (Nishida 1980), and western lowland gorillas (Williamson *et al.* 1988). These and other reports indicate that apes' behaviour toward water bodies in the wild might be adaptive—they avoid deep water bodies and are extremely cautious when entering even shallow water. To my knowledge, there are no observations of apes drowning in their wild habitats.

Nishida investigated the question if hydrophobia is innate or learned in wild chimpanzees. He concluded that it is probably not innate, but that young chimpanzees show fear from most new objects or situations. It is the mother's attitude which teaches the infant whether an object is dangerous or not. As many wild chimpanzees have little direct contact with water bodies, it is possible that young chimpanzees never learn a specific attitude towards water and retain the reluctance to enter it (Nishida 1980). Similarly, in rhesus monkeys the fear of snakes is not innate, but has to be taught by the mother (Byrne 1999, 58). However, even in hand-raised apes, where human foster mothers did not teach a negative attitude towards water, fear of water can occur. Maria Hoyt reported that the hand-raised female gorilla, Toto, surprised her when she took her to a backyard swimming pool. Toto reacted with panic when Hoyt entered the water and tried to pull her out (Hoyt 1941, 114-115). Anna Mae Noell reported a very

similar reaction by the 3-4 year old chimpanzee Kongo, when she took him to the beach. She swam out with Kongo on her shoulders, when Kongo panicked and tried to jump back to the beach. He almost drowned and had to be pulled out of the water (Noell 1979, 144). Similarly, the chimpanzee, Snookie, reacted with panic every time when he saw Noell's six-year old son Ben walking towards the water. One day Ben fell into the water and Snookie saved him by pulling the child out with a foot. Snookie also showed signs of fear and stress when riding a boat or crossing a bridge (Noell 1979, 21).

In humans fear of water is often more present in mothers who fear that their infants can drown than in the infants themselves. Otherwise, fear of water in human adults is generally limited to non-swimmers, as discussed in the review on human aquatic activities. In Western societies fear of water occurs mostly only after an unpleasant experience like a near drowning (Gabler 1982; Greuter 1995; Knöpfel 1982; Whiting 1970).

The evident contrast between the number of observations of drowning in wild and captive apes indicates that factors found only in artificial environmental settings influence certain aspects of their behaviours towards water. Water is often used to constrain animals in semi-free ranging and captive conditions, exposing them more frequently to water bodies than wild conspecifics. Similarly, highly arboreal apes spend more time on terrestrial substrate in captivity than in the wild, leading to a more frequent exposure to water than with wild conspecifics (Russon *et al.* 2010a). Captive animals often do not have experience with deep water bodies when first released into a new zoo exhibit (van Hooff 1973). When released, apes are often immediately attacked by other individuals and might jump or fall into the water moat and drown (Armstrong Mdoda, Johannesburg Zoo; Gerry Creighton, Dublin Zoo; Bev Carter, Toronto Zoo, pers. comm.).

These and other reports on drowning apes (see chapter 4.3.3) reveal that apes exposed to deep water do not show fixed rhythmic action patterns of innate swimming, as observed in the doggy paddle of terrestrial mammals. After falling in water and losing contact with solid substrate, apes tend to assume a variety of inefficient postures, to move their limbs in an uncoordinated way ("fumbling"), and to be spatially disoriented. As shown, these uncoordinated reactions in water are atypical for other terrestrial vertebrates. As the lack of innate swimming is not affected by learning or environment, it demands evolutionary explanations.

CHAPTER FIVE – AQUATIC ACTIVITIES IN HUMANS

5.1 Introduction

How do human aquatic activities compare to other hominoids' aquatic activities? Intuitively, this question may be answered with reasonable certainty by stating that humans interact more often and more intensively with water than the other hominoid species.[66] However, as far as can be assessed, there is no comprehensive literature review or other investigations focusing on the extension of aquatic activities in a representative number of today's human cultures. To establish to what extent bathing, swimming and diving behaviours are practiced among human populations, a systematic collection of primary data in a representative number of human cultures would be necessary. As this is not feasible in the framework of the present thesis, I performed a literature review on the topic – an approach similar to the one taken for the aquatic activities in non-hominoid primates and apes. The aim of this review is to describe a representative number of different patterns of human water contact. The review focuses on those aspects of aquatic behaviours which imply a strong bodily contact to water, which is inevitable during bathing, swimming and diving activities. Drinking and activities connected to sophisticated technology were excluded here.

Several works were written on the development of baths and bathing in different times and different populations, as for instance in ancient Greece (Gell & Gandy 1852; Weber 1996), in ancient Rome (Cameron 1772; Manderscheid 1988; Weber 1996), in Germany during the Middle Ages (Martin 1906) and other regions (Scott 1939; Spörry 1920). Basically, historical investigations of swimming in ancient times are based on Hellenic, Roman and Greek divine myths, poems, heroic sagas, architectural findings and archaeological evidence. Stylized representations of humans bathing and swimming are known from cave paintings, coins, vases, murals, hieroglyphs, paintings, bas reliefs and small sculptures (Brendicke 1930; Mehl 1927; Mehl 1950; Orme 1983; Sinclair & Henry 1893; Thomas 1904; Weber 1996). Today, sea bathing is basically regarded as a recreational activity. However, it was the medical aspect of coastal environment (i.e., breathing the air of the seaside, bathing in and drinking seawater) which gave the initial impulse for the early development of the sea bathing culture. The work of Richard Russell *A Dissertation on the Use of Sea Water in the Diseases of the Glands*

[66] This was an assumption that I expressed in an unpublished diploma work (Bender 1999).

(Russell 1753), first published in Latin, was pivotal to this phenomenon.[67] Trips to the coast were initially restricted to the privileged classes (Scott 1939) and grew out of the old tradition of bathing for therapeutic purposes and drinking cures with "curative water", which was characteristic for several cultures (Krížek 2010; Martin 1906; 1936a; 1936b; 1936c; 2008; Rapp 1976; Spörry 1920; Von Hahn & Von Schönfels 1987). In England, the seaside as a place of leisure became popular after the arrival of the railways in the 1830s and 1840s (Elborough 2011; Hannavy 2003; Parr 2011; Prignitz 1993); followed by the Baltic and North Sea regions (Bengen & Wördemann 1992; Prignitz 1977; Prignitz 1993).

Interestingly, despite the great interesting in the history of swimming and bathing, I was not able to find any specific review on swimming and bathing in tribal people.[68] In tribal people, interactions with water often occur in natural water bodies, often in connection with other activities which are essential for their subsistence (as, for instance, gathering food or crossing water bodies by wading or swimming). Another aspect of the interaction with water in these groups is related to swimming techniques, which in these cultures are less dictated by rules, as for instance, learning to swim according to standardised Olympic styles. The focus on tribal people also excludes human diving which is dependent on breathing devices or other forms of sophisticated technical aids. This applies to the use of diving bells, diving helmets (Augustinski 1994), and self-contained underwater breathing apparatus (SCUBA) (Cousteau & Dumas 1981). Although free diving observed in 'natural divers' gathering different sea products are considered here, free diving performed in a competitive context (Andres-Brümmer 2005; Mayol 1986; Pelizzari & Tovaglieri 2004), spearfishing performed as sport (Bracony 1975; Santarelli 1983) and diving during snorkeling are not included in the present review.

[67] For a reference about bathing in the sea in Europe before Russell's publication see Walvin (1978, 16-20); and about the "discovery" of the coastal environment in Europe in 18th and 19th century see Corbin (1990). Several discussed different aspects of seaside bathing (Atterbury 2008; Ayriss 2012; Bengen & Wördemann 1992; Berman 1977; Booth 2001; Braggs & Harris 2006; Ferry 2009; Gray 2006; Hannavy 2003; Holfelder 1996; Kimpel & Werckmeister 1995; Parr 2011; Pertwee 1999; Prignitz 1977; Prignitz 1993; Prignitz 1998; Timm 2000; Travis 1993; Travis 1994; Walton 2000).

[68] In German, the term "*Naturvölker*" represents an overriding notion of humans living a state of "closeness to the nature" and less dependent on sophisticated technology when compared (for instance) with Westernized societies. To my knowledge, the term *Naturvölker* does not have lexical equivalents in English. The terms "indigenous people", "tribal people", "technologically less sophisticated (or less advanced) societies" or "primitive people"; the last term justifiably considered as offensive and obsolete (Anonymous 2013) are the common terms used in ethnological works. The term "tribal people" will be used here as synonym for the German term, although it does not fully reflect it.

It is important to note that similar patterns of water use might occur both in Westernized and tribal people. For instance, children playing in water or the use of water in religious rituals are widespread in both groups, and any attempt to regard these activities as different are probably highly artificial. Furthermore, "Westernized cultures" – referring to heritage that is associated with Europe (Hayes 1964) is a broad term. Humans in different regions of the world with Westernized cultures interact with natural water bodies in a variety of ways. In the USA, for example, certain creeks, ponds or rocky gorges used for the purpose of swimming, bathing and playing are called "the old swimming hole". Swimming holes are an important aspect of the cultural heritage in the USA, and since the turn of the 20th century they are recurring motifs in literature and artistic work (Peters 2010). Similar patterns of water use can be observed in other countries. For example, during the summer in small villages in south Paraná, Brazil, boys regularly visit sections of creeks which are known as suitable for swimming. Without the possibility of participating in a swimming course, children in these groups swim using techniques acquired without systematic training. Swimming styles often displayed are dog paddle and styles characterised by an exotic note instead of efficiency.[69] In metropolises, such as Curitiba, Paraná, Brazil, on hot days, street children play regularly in water from artificial lakes or fountains in parks (own observation). In the metropolitan area of Curitiba, children regularly swim in dams, rivers and holes filled up with rain water (called *cavas* in Brazil) in sand mines (Rosa 2011). Similar patterns of water use occur in other regions of the Westernized world. This applies not only to places where public and private swimming pools are not available, but also in countries with a long tradition of swimming pools (Ayriss 2012; Parr 2011). These and other facts suggest that it is difficult to draw clear boundaries between patterns of water use in Westernized and tribal people. The focus on tribal people in the present work is basically a matter of delimitation of the scope of the investigation.

5.2 Methods

A systematic literature search on the reports of bathing, swimming and diving by humans was performed here, using the online database eHRAF Word Cultures

[69] Example of these exotic swimming styles are: (a) *moinho de vento* (wind mill, a kind of rudimentary crawl without lateral breathing); (b) *motorzinho* (little motor, a kind of highly inefficient dog paddle, coiling the arms frenetically half submerged in water in front of the body, mimicking a motor); and (d) *arrancão* (an inefficient technique, in which the legs execute a dolphin-like kick, the arms moving simultaneously in front of the body, not leaving the water in the recovering phase) (own observation; see also (Alves 2013)).

(http://ehrafworldcultures.yale.edu) from 26 June to 3 October 2012. This database is focused on cultural and social aspects, and run by the Human Relations Area Files (HRAF), an internationally recognised organisation in the field of cultural anthropology based at Yale University, New Haven, USA. In this database, information is divided into cultures and ethnic groups which are categorised into major geographic regions (Africa, Asia, Europe, Middle America and the Caribbean, Middle East, North America, Oceania, and South America).

According to the eHRAF website, 257 cultures[70] were selected for the online database, representing indigenous and traditional cultures of all world regions (see Table 5.1). The cultures were selected to represent the range and variety of language, history, economy, and social organisation. They cover all major world regions and all major ecological settings. Additionally, the database aims at adequate quantitative and qualitative literature coverage for each culture.

I asked Carol Ember, president of Human Relations Area Files at Yale University, how representative are the data here used for humanity as a whole. She answered:

> The question asked is not that easy to answer. First, there is no definitive list of the world's cultures as yet that can be used as a sampling frame. Therefore, without a sampling frame, it is not possible to have a random sample of the world's cultures. Second, the HRAF Collection of Ethnography (with eHRAF World Cultures as a subset) does not claim to be a random sample. Therefore it does not claim to be a representative sample. However, in the absence of an adequate sampling frame, most researchers have chosen a cross-cultural sample, not of their own choosing, to sample from. (Carol Ember, pers. comm.)

In the context of this thesis, it is relevant to note and stress the evidence that the eHRAF database was not designed with a specific aim of excluding or including data on aquatic activities; consequently no bias in this respect may be expected.

[70] The eHRAF was built up historically, using data available in the literature, and is growing constantly. When the present research was carried out from 26 June to 3 October 2012, 257 cultures were included. Now (25 July 2014), the number has increased to 289. According to the eHRAF website, "Every year 20-30 cultures with approximately 40,000 pages are added to eHRAF" (http://hraf.yale.edu/online-databases/ehraf-world-cultures/cultures-covered/by-regions-and-subsistence/).

Table 5.1 Cultures included in the eHRAF database

Africa:	
Central Africa:	Azande, Barundi, Mbuti, Mongo, Rwandans, Teda.
Eastern Africa:	Amhara, Bagisu, Banyoro, Bena, Chagga, Ganda, Gikuyu, Gusii, Luo, Maasai, Nuer, Nyakyusa and Ngonde, Shilluk, Somali, Turkana.
Northern Africa:	Berbers of Morocco, Fellahin, Libyan Bedouin, Shluh, Tuareg.
Southern Africa:	Bemba, Betsileo, Khoi, Lakeshore Tonga, Lozi, Ovimbundu, San, Tanala, Tsonga, Zulu.
Western Africa:	Akan, Bambara, Dogon, Hausa, Igbo, Kanuri, Kpelle, Mende, Mossi, Tallensi, Tiv, Wolof, Yoruba.
Asia	
Caucasus:	Abkhazians.
Central Asia:	Ghorbat, Hazara, Inner Mongolia, Karakalpak, Kazakh, Kyrgyz, Lepcha, Mongolia, Pamir Peoples, Pashtun, Sherpa, Tajiks, Tibetans, Turkmens, Uzbeks.
East Asia:	Ainu, Korea, Miao, Monguor, Okayama, Okinawans, Taiwan Hokkien, Yi.
North Asia:	Chukchee, Koryaks, Nivkh, Yakut.
South Asia:	Andamans, Badaga, Baluchi, Bengali, Bhil, Burusho, Garo, Gond, Khasi, Santal, Sinhalese, Tamil, Toda, Uttar Pradesh, Vedda.
Southeast Asia:	Alorese, Balinese, Central Thai, Eastern Toraja, Iban, Ifugao, Javanese, Malays, Mentawaians, Rungus Dusun, Semang, Southern Toraja, Vietnamese.
Europe	
British Isles:	Highland Scots.
Scandinavia:	Early Icelanders, Icelanders, Saami.
Southeastern Europe:	Bosnian Muslims, Croats, Greeks, Montenegrins, Serbs, Slovenes.
Southern Europe:	Basques, Imperial Romans.
Middle America and the Caribbean	

Caribbean:	Cubans, Dominicans, Island Carib, Jamaicans.
Central America:	Garifuna, Kuna, Miskito.
Central Mexico:	Nahua, Zapotec .
Maya Area:	Mam Maya, Maya (Yucatán Peninsula), Tzeltal.
Northern Mexico:	Huichol, Tarahumara.
Middle East	
Middle East:	Basseri, Bedouin, Iran, Israelis, Kurds, Lur, Palestinians, Rwala Bedouin, Turks, Yemenis.
North America	
Arctic and Subarctic:	Aleut, Alutiiq, Chipewyans, Copper Inuit, Innu, Ojibwa, Western Woods Cree.
Eastern Woodlands:	Cherokee, Creek, Delaware, Iroquois, Mi'kmaq, Seminole, Winnebago/Ho-Chunk.
Northw. Coast and Calif.:	Chinookans of the Lower Columbia River, Nuu-chah-nulth, Nuxalk, Pomo, Quinault, Tlingit, Yokuts, Yuki, Yurok.
Plains and Plateau:	Assiniboine, Blackfoot, Comanche, Klamath, Omaha, Osage, Pawnee, Stoney.
Regional and Ethnic Cult.:	African Americans, Amish, Arab Americans, Arab Canadians, Basque Americans, Cajuns, Chicanos, Chinese Americans, Chinese Canadians, Cuban Americans, Haitian Americans, Italian Americans, Italian Canadians, Korean Americans, North American Armenians, North American Hasidic Jews, North American Hmong, Puerto Ricans (Mainland), Sea Islanders, Serbian Americans.
Southwest and Basin:	Havasupai, Hopi, Mescalero Apache, Navajo, O'odham, Tewa Pueblos, Ute, Western Apache, Zia Pueblo, Zuni.
Oceania	
Australia:	Aranda, Tiwi.
Melanesia:	Kapauku, Kwoma, Malekula, Manus, Orokaiva, Santa Cruz Islanders, Trobriands.
Micronesia:	Belau, Chuuk, Marshallese, Ulithi, Woleai Region, Yapese.
Polynesia:	Hawaiians, Lau Fijians, Maori, Marquesas, Samoans, Tikopia, Tongans.

South America

Amazon and Orinoco:	Bakairi, Barama River Carib, Canelos Quichua, Jivaro, Mundurucu, Nambicuara, Ndyuka, Saramaka, Shipibo, Sirionó, Ticuna, Trumai, Tukano, Warao, Yanoama.
Central Andes:	Aymara, Inka, Mapuche, Otavalo Quichua, Quito Quichua, Saraguro Quichua.
Eastern South America:	Bahia Brazilians, Bororo, Guaraní, Tapirapé, Tupinamba, Northwestern South America, Kogi.
Southern South America:	Abipón, Mataco, Ona, Tehuelche, Terena, Yahgan.

The material of the eHRAF database includes books, articles, and dissertations and is largely descriptive, mostly as the result of field observations by professional sociologists, but also by early explorers. Caution is necessary when interpreting reports of early explorers, as the descriptions are sometimes rather subjective and judgmental – a product of the Eurocentrism of the time.

The full-text sources are subject-indexed (and therefore searchable) at the paragraph level, using subject category codes of the classification scheme "Outline of Cultural Materials" (OCM, see eHRAF website for further explanations). For the present investigation the keywords swim*, diving, and bath* were searched. The truncation allows for extensions like swimmer, swimming, bather, bathing, bathed, etc. Each search term was combined with relevant OCM categories: bath* was combined with 'Personal Hygiene', swim* with 'Athletic Sports', 'Commercialised Sports', 'Locomotion', and 'Transmission of Skills'. The term 'diving' was combined with 'Athletic Sports', 'Commercialised Sports', 'Locomotion' and 'Marine Industries'. Aquatic behaviours solely related to medical treatment, and to religious or traditional rituals were not recorded. Furthermore, data on the chosen aquatic behaviours in was collected in additional literature from the libraries of the Universities of Bern, Basel and the Witwatersrand, and my personal library (122 ethnological books, book chapters and papers reporting on cultures from all world regions).

All documents of the eHRAF database reporting on the selected aquatic behaviours were collected and divided by aquatic behaviour and by geographic region (complete data from a total of 637 references available upon request). For each category the number of represented

cultures was counted. This method allowed for recording and quantifying the presence of chosen behaviours by geographic region. However, for cultures in which certain behaviours were not reported, it does not mean that they do not occur. The present review reflects, therefore, a very conservative estimate of the occurrence of aquatic behaviours. However, if it can be assumed that the reporting of the chosen behaviours does not differ drastically between geographic regions, a cross-regional comparison of occurrences can be performed (see Table 5.2).

Furthermore, patterns of aquatic activities in human populations that emerged from the data collected were qualitatively analysed, such as differences between sexes or age groups, learning patterns in children, correlations of behaviours with climatic factors or cultural barriers for aquatic activities. Here, the additional literature from libraries was also included. For each group of behaviours, several chosen examples were given, for illustrating purposes.

5.3 Overall results from the eHRAF database review

Table 5.2 summarises the number and percentages of the cultures in which bathing, swimming and diving were described in the eHRAF database. Other literature was not considered here, so that percentages of occurrence of behaviours within this dataset could be calculated. For swimming, most researchers reported the presence as well as the absence of this behaviour. Table 5.2 records both the presence and the absence of this specific behaviour. For bathing and diving, the total absence of these behaviours was rarely described and so the total numbers of reported cultures were given, without differentiation.

Table 5.2 Cultures for which swimming, diving or bathing was reported

Region	Nr of cultures	Bathing		Do swim		Do not swim		Diving	
		nr	%	nr	%	nr	%	nr	%
Africa	49	34	69	18	37	2	4	4	8
Asia	56	35	63	17	30			4	7
Europe	12	8*	67	3*	25			1	8
Middle America**	14	10	71	4	29			1	7
The Middle East	10	6	60	2	20			1	10
North America	41 ind.	36	88	21	51	4	10	11	27
	20 imm.	7	35	4	20	1	5		
	(61 total)	(43)	(70)	(25)	(41)	(5)	(8)	(11)	(16)
Oceania	22	19	86	16	73			12	55
South America	33	30*	91	18*	55	2	6	7*	21
Total	**257**	**185**	**72%**	**103**	**40%**	**9**	**4%**	**41**	**16%**

For North America, numbers and percentages are given for indigenous (ind.) cultures and for immigrant (imm.) populations. In brackets the total for North America is given, which is excluded from the total of the table

*Of which 1 each is historic, Imperial Romans in Europe and Incas in South America

**Including the Caribbean

Aquatic activities were reported in all cultures. Bathing was mentioned in 72% of all indigenous cultures (60%-91%), swimming in 40% (20%-73%) and diving in 16% (7%-55%). The majority of cultures in which the aquatic activities were described were found in North America (indigenous cultures), Oceania and South America, with bathing at 86%-91%, swimming at 51%-73% and diving at 21%-55%. In North America, bathing is often linked to steam baths. In the other geographic regions (Africa, Asia, Europe, Middle American and the Caribbean, and the Middle East) the aquatic activities are still described regularly, but in smaller numbers: bathing was at 60%-71%, swimming was at 20%-37%, and diving was at 7%-10%. Interestingly, Middle America and the Caribbean do not follow the pattern of the neighbouring regions (North and South America), but instead follow the patterns of other regions (Africa, Asia, Europe and the Middle East). The most aquatic activities were reported for Oceania, with 86% of cultures reported as bathing, 73% as swimming and 55% as diving.

For immigrant populations in North America, aquatic activities are described as frequently as in their regions of origin, or less frequently. One reason might be the poor socio-economic conditions linked to a poor access to clean water often described in these groups. Chavez, for

instance, reports on illegal immigrants in the USA in the 1990s. In a mobile home park next to El Camino Real, illegal Chicano immigrants had to bath in trash containers (Chavez 1998, 90). An account of the conditions of Italian immigrants in the USA at the end of the 19th and the beginning of the 20th century reports on buildings inhabited by Italian immigrants, where the plumbing was so poor that residents were without water for several hours each day. Bathing and cleaning facilities were lacking (Pozzetta 1991, 117). Another reason for a number of non-swimmers among North American immigrants was the maintenance of cultural beliefs and customs from their countries of origin. Kamen reported that swimming was an approved activity in New York City's schools. Several times a week during the summer, the children were taken to a local pool, reserved exclusively for use by the Yeshiva (Jewish school), and given swimming instructions. However, the more conservative members among the Hasidic groups disapproved of such behaviour (Kamen 1985, 50).

5.4 Differences and similarities between cultures

From this section onwards, results from the eHRAF database as well as additional literature from the library research are included.

5.4.1 Perceptions of the "amphibious character" of tribal people in early reports

Before the presentation of the results, some remarks on the reliability of early ethnographic accounts are needed here. As stated in Appendix D, until the early 20th century, naturalists, travellers, missionaries and explorers had a tendency to depict primates with typical human features. Similarly, naturalists, travellers, missionaries and explorers of this time had the tendency to describe non-European and technologically less sophisticated people as bearing animal-like physical and behavioural traits. The perceived linkage between tribal people and non-human creatures was influenced by different factors. Typical physical and behavioural features which characterize humans were mixed with typical Caucasian traits (a result of the Eurocentric view of this time) and used in an arbitrary system of comparison between European and non-European cultures. Consequently, tribal people were often caricatured regarding features like body hair, nasal aperture, orthognathism, upright posture, body strength and intelligence. Non-Europeans were sometimes described as more skillful than Europeans concerning their abilities to swim, dive, climb trees, or run. Although not all alleged differences between Western naturalists and tribal people completely lacked a factual basis, it is often difficult to discern if the facts were enriched by vivid phantasy or were the result of a rather objective evaluation from an observer of the time. Examples of reports

difficult to evaluate were published on the now extinct Agaiambu tribe of the north-east coast of Papua New Guinea, and evident in statements by Lapérouse on natives of the Solomon Islands (see chapter 5.4.3). However, these reports are rather exceptional when compared with other statements expressing a high degree of familiarity with water among tribal people (see chapter 5.4). Most statements on "amphibious races" are often the expression of genuine admiration or astonishment from naturalists less used to use water for hygienic purposes[71] or for leisure[72] than several non-European cultures of tropical regions.

5.4.2 Bathing

Differences concerning bathing for the purpose of hygiene

As evident from the numbers in the table above, bathing is described regularly in all parts of the world. A typical example is given by Abelove on the Shipibo Indians in South America:

> The day begins just before sunrise when the villagers go down to bathe and defecate in the river. Women bathe with their young children; men bathe alone; older children bathe together. Mothers return to their kitchens and stir up the fire to keep themselves warm until the sun comes up. While they begin to prepare breakfast—some left-over stew or merely roasted plantains—the men finish bathing. (Abelove 2000, 22)

Napoleon A. Chagnon reported on the indigenous Yanoama[73] [or Yanomami] in Brazil that they work in their gardens until the latee morning. Afterwards they retire because it is too humid and hot to continue with this strenuous work. Chagnon reported further: "Most of them bathe in the stream before returning to their hammocks for a rest and a snack" (Chagnon 1992, 130). On the next page he reported on bathing after the use of drugs:

> If the men return to their gardening, they do so about 4:00 p.m., working until sundown. Otherwise, they gather in small groups around the village and take hallucinogenic drugs in the

[71] Standards concerning the use of water for hygiene purposes in Europe changed radically in the last two centuries (Shove 2003).

[72] A far larger number of people from Westernized countries in 19th and early 20th century were probably not able to swim when compared with today's populations. In 1950, Kurt Wissner wrote that *ca* 80 % of Austrians were not able to swim (Wiessner 1950), a number which is probably representative for other central European countries at this time. Some decades later, in Switzerland, only 4% of children aged 10-14 were, according to their self-evaluation, not able to swim or were poor swimmers (Lamprecht & Stamm 2009, 4). However, swimming ability strongly varies among the regions of Switzerland, and self-evaluations do not reflect precisely objective evaluations. For instance, an evaluation of the swimming ability of children in primary schools in the canton of Luzern, Switzerland, showed that 11% of the children were not able to swim (Lindegger 2010).

[73] eHRAF's terminology is followed here.

> late afternoon shadows, chanting to the mountain demons as the drugs take effect. This usually lasts for an hour or so, after which the men bathe to wash the vomit or nasal mucus off their bodies. (Chagnon 1992, 131)

Another example of an author mentioning bathing and hand washing is from observations made of the Ganda people in Africa:

> Personal cleanliness and tidiness is stressed in Buganda. Although water must be carried from wells, which are often distant, a daily bath, be it only a sponge bath, is customary for an adult. Hands are washed before eating. (Ainsworth 1967, 71)

An example from Asia shows the similarities of bathing habits, such as in the Balinese:

> Every member of the family is accustomed to go down at least once a day to the river or the bathing-place for his bath, and many must climb up and down several times in a day—the women and girls carrying water for household needs, the men going to and fro in their work in the steeply terraced rice-fields, the small boys escorting their special charges, the ducks and the water buffalo, down from the dry ground for their daily immersion. (Belo 1936, 123)

Adults of the Ifaluk people of the Central Caroline Islands in Oceania wash in the morning, while young people wash in the afternoon (Burrows & Spiro 1957, 315). In Africa, the day for the Zulus „usually began with bathing. Most Zulus bathed at least once a day, with a passion for cleanliness that mystified the bath-shy British“ (Edgerton 1988, 29). The Mbuti pygmies „keep their bodies scrupulously clean, and the favorite recreation of the children is playing about in the shallow streams“ (Turnbull 1965, 212). An account first published in French in 1665 from the Island Carib states:

> The first one to awake at the cock's crow plays his flute, and the others imitate him as they awaken. After this they go to bathe in the river. The women and children go at a different time. Because the river is cold they make fires by groups in two or three places where they warm themselves. If they are soaked by sea water or rain, or if they are dirty or overheated by some exertion, they return to wash themselves again. Besides this they never fail to go bathing at noon and in the evening. I think that these baths contribute the most to the preservation of their health, and so do their fasts when they are moderate. (Breton 1958, 22)

With the Chuuk in Oceania “[l]aundry and bathing are done in tiny streams or in shallow pools along the course of the river” (Marshall & Marshall 1984, 38).

Cases of bad hygiene were described in 54 cultures (8 in Africa, 20 in Asia, 1 in Europe, 2 in the Middle East, 12 in North America, 2 in Oceania and 9 in South America). However, such reports have to be considered with caution, as early explorers often described indigenous populations with pejorative statements, while the same culture might be described as 'clean' by modern researchers. An example is provided by Speiser, who reported on the inhabitants of the islands Vanuatu. According to Speiser, the inhabitants of the coast were clean people, washing themselves regularly. The inhabitants of the interior, however, he reported as covered with crusts of dirt. He attributed this condition to the lack of water (Speiser 1923, 69).

The problem of biased reporting was discussed by A.T. Bryant in connection to the Zulu people:

> It is a disposition of nature that, in the make-up of a gentleman, he will respect his person as he does also his behaviour; and so we find both these qualities conspicuous in the Zulu character. They were innately a cleanly and tidy people, and disorder and unsavouriness were distasteful to them. And yet, in actual fact, it must be owned, they often failed to reach even their own lowly standard. Whey they failed has often been plaintively told us: si-y'-Ahlueka, it-is-beyond-our-power. They were unable to improve their condition and to rid themselves of the dirt and untidiness amidst which they lived, owing to the complete absence among them of all those commodities and conveniences with which we have been able to supply ourselves – due, in their case, no doubt, to their innate lack of all inventive power. Absence of soap and other sanitary helps was sorely felt by them; though they never said so, being entirely ignorant that anything better than what they had, ever existed. (Bryant 1949, 235)

Bryan, however, criticised interpretation of the character of the Zulu people based on superficial knowledge. He wrote:

> This intellectual poverty had gone far to mislead Europeans, unfamiliar with their innermost thoughts and nature, into the false opinion that they are a dirty race, perfectly content with their squalid surroundings and possessing no desire to see them improved. In reality, the truth is that no people accepts more greedily the common benefits of civilisation, so soon as they are brought within its reach. A great part of the day, in former times, even up to 50 years ago, was spent by the young men and girls in dressing and decorating their persons, and it was a discomfort to them to miss their frequent bathe in the neighbouring stream, where such existed. (Bryant 1949, 235)

Bryan described gender specific bathing rituals in streams and paterfamilias' privileges concerning bathing:

> A well-bred man always commenced his bath by washing first his head, then following with the arms, and finally the upper and lower body. A woman likewise commenced with the head, but next proceeded to the body and legs, finishing up with the arms. For either of them to wash like the other sex, would have appeared, to Native eyes, improper, even ridiculous. When bathing, companions often assisted each other by washing one another's backs (ukuBúxunga), in which process the leaves of the iNkweza tree (Kraussia floribunda) were frequently employed. Save in the washing of infants and the sick, they never used warm water, as do some other Negro peoples [.] Paterfamilias, already well on in years, was often disinclined to walk down the hill to the stream and then trudge back again; so he had his washing-basin (umCengezi) brought into the cattle-fold and there, assisted by a boy or by his wife, took his bath. (Bryant 1949, 235-236)

Cultures in which bathing is described as rare, are often found in cold climates or do not have access to clean water. Examples are the Sherpa in Asia (Kumwar 1989, 146) or the Aymara in South America (La Barre 1948, 45), both living in extremely cold climates in the Himalaya or the Andes. However, cold climate or cold water is not a barrier to regular and extensive aquatic activities in many other cultures. In the case of the Mapuche Indians in South America, for instance, adults often bathe daily, even during the winter season. They prefer to bathe in flowing water, as in rivers or creeks or under waterfalls or at springs (Hilger 1957, 58). In North America especially, children are often bathed in cold water in the belief that this will make them strong, a habit sometimes also shown by adult men. According to Goodwin and Goodwin, Western Apache children from the age of eight or ten years onwards had to swim in cold water, in the conviction that this would make them physically strong. They had to run to the river, jump in and remain there for several minutes. The bathing continued in summer and winter, and in cold weather the children often had to break the thin ice before they could enter the river (Goodwin & Goodwin 1942, 461). A similar custom was observed, among others, with the Hopi (Dennis 1940, 41) and the Blackfoot people (Lancaster 1966, 118). The belief that bathing in cold water strengthens the body was already expressed in early times, like by Lord Monboddo in his *Antient Metaphysics* (publ. 1779-1799), where he wrote on the benefits of frequently bathing as remedy for the mischief of clothing. He ascribed a long life to bathing in a river three times every day (Monboddo 1784, vol. 3, 87-88).

In some cultures, bathing habits changed over time, increasing in frequency. Such a change was described among the Mongolians in Asia (Far Eastern and Russian Institute 1956, 34, 415-416; Goldstein & Beall 1994, 93) and among the Badaga in Asia (Hockings 1980, 36). The Marshallese in Oceania also changed their washing habits over time: “The islands have a long history of skin diseases, generally attributed to a lack of personal cleanliness. Natives now spend much time each day laundering their clothes and bathing in fresh water (soap remains one of the most desirable trade items despite big deliveries in the islands since the war)“ (Mason 1947, 22).

In other cultures, the introduction of clothes by Western explorers or missionaries was assumed to worsen the hygiene of the people in the beginning. The Andamans in Asia, for instance, were described as clean and healthy people, a fact attributed to their nakedness: „To cover them with clothes would endanger their health. Nakedness inures them to the sudden changes of temperature so frequent in Little Andaman and preserves them from catching cold when sleeping, uncovered, on their rough, unprotected bed of boughs. As with primitives all over the world, clothes make them miserable and, I may add, very ungainly and dirty“ (Cipriani 1961, 485). A similar experience was described for the Guarani in South America: „From the point of view of hygiene, the use of clothing is highly detrimental, for as soon as the Indian puts on garb of European type the cleanliness of the body leaves much to be desired; it is as though the clothing made baths dispensable. Washing the clothes, too, is a pattern poorly integrated in the culture. There are many Indians who, as soon as they get a piece of clothing, put it on without losing any time, using it day and night, until it falls apart“ (Schaden 1969, 40).

Bathing babies was often reported. Here is one example on Ganda, in Africa: for “the small children daily bath is routine for everyone, but babies are bathed even more frequently. After mouth-rinsing, a bath was traditionally the first experience of the newborn child” (Ainsworth 1967, 71). Other reports on bathing babies can be found, among others, on the Ibos of Nigeria: (Basden 1966, 63); the Kanuri in Nigeria: (Cohen 1967, 55); and for the Zapotec-speaking people in Oaxaca, Mexico: (Clews Parson 1970, 78). People who are known to bath irregularly often do not bath their babies. One example reported on two Yanoama tribes in Brazil, the Surara and the Pakidai:

> Regular bathing, washing of the face and hands, and cleaning the finger and toe nails are unknown; this is also true for babies, who are often covered with a veritable crust of dirt. Nor do they brush their teeth or ever rinse their mouths. Yet I was never aware of an unpleasant body odor or bad breath on the Indians, and until an advanced age their teeth are dazzlingly white and sound. While hunting or gathering, however, if men and women are obliged to cross a brook or small river, they gladly utilize the opportunity to take a refreshing bath, and the same is true when female members of the tribe fetch water. A bath is greatly appreciated by children and young people, but not at all by older persons. (Becher 1966, 195)

In a report of 1921 on Mongolic people by Maiskii (here quoted from a translation published in 1975) it is written:

> On the third day after the birth, the child is given a name. This is done with the participation of a lama, but without any special ceremonies. Only on this day is the child washed: the Khalkhas wash it in warm mutton broth; the Dürbets, in warm boiled water or also in some broth. For the Khalkhas, this washing is the only bath he will ever know. The Dürbets are somewhat more cleanly: they wash their children up to the age of 2 – 3, but then they also stop (Maiskii 1975, 131)

Cases of bad hygiene of babies were also reported concerning Sherpa people of eastern Nepal (Kumwar 1989, 191), the Yahgan in Tierra del Fuego, South America (Gusinde 1961, 74-77), and with respect to the Nyasongo in Kenya (LeVine & Lloyd 1966, 141-142). Two authors reported on the Nivkh, an indigenous ethnic group inhabiting the Sakhalin Island and Russia's Khabarovsk Krai. According to the report, adult and children rarely bath, and only "nursing infants are bathed twice daily" (Seeland & Schütze 1882, 32)

Differences in bathing between sexes

Water contact is not the same in both sexes in all cultures. In some cultures, women bath more frequently than men as they regularly go to water sources to take water, as for instance in the case of the Rwandans (Czekanowski 1959, 123) or the Mossi (Mangin 1959, 78) in Africa. In other cultures, decency is a barrier for women to bath regularly, while this is not so much the case for men, as for instance with the Tamil in India (Djurfeldt & Lindberg 1975, 97).

As already mentioned above, men and women do not often bath together. In respect of the Balinese, Asia, for instance, "where there are gushing springs, bathing places are constructed, with walls dividing off the place of the women from that of the men. When the rivers are used

for bathing, the sexes divide into groups, the men taking the upstream position, the women the downstream“ (Belo 1936, 136). Similarly, in 1822 Dobrizhoffer reported on the Abipon Indians in South America:

> The custom of bathing in a neighbouring stream is agreeable to them, and practised every day, except when the air is too cold. But do not imagine that as sylens and dolphins are seen sporting on the same waves in the ocean, males and females swim and wash in the same part of the lake, or river. According to the Abiponian custom, the different sexes have different places assigned them. Where the women bathe, you cannot find the shadow of a man. (Dobrizhoffer 1822, 139)

The commonest exceptions of this separation rule are married couples or small children, who often are allowed to bath together. Only in very few cultures do adults of both sexes bath jointly, as for instance the Garifuna of Mittle America:

> Climatic conditions in Central America minimise the protective role of clothes. Children are allowed to go naked until they are five or six, and until adolescence dress only scantily. Adults are supposed to keep their bodies covered for reasons of decency, but their love of fresh water and cleanliness overcomes their desire to conform to Western patterns of behavior. During the warm season, men and women bathe in the rivers together, often wearing only loincloths. (Coelho 1989, 125-126)

Bathing as recreation

Recreation in water is described in many cultures, especially concerning children, but also with respect to adults. The Tehuelche in South America, for instance, “did a great deal of recreational swimming and diving, at which they were very proficient“ (Cooper 1946b, 157). In the case of the Mapuche “[m]en, women, and children were excellent swimmers; they indulged in this exercise partly for cleanliness and Spartan self-training, and partly for recreation” (Cooper 1946a, 739). Lévi-Strauss reported on the Nambicuara that “women and children often bathe together for amusement, and sometimes a fire is lighted before which they crouch to warm themselves on coming out of the water while they playfully exaggerate a natural shivering” (Lévi-Strauss 1948, 16). In Hawaii, water sports were reported as very common:

> They have a variety of games, and gambol as fearlessly in the water as the children of a school do in their playground. Sometimes they erect a stage eight or ten feet high on the edge of some

> deep place, and lay a pole in an oblique direction over the edge of it, perhaps twenty feet above the water; along this they pursue each other to the outermost end, when they jump into the sea. Throwing themselves from the lower yards, or bowsprit, of a ship, is also a favourite sport, but the most general and frequent game is swimming in the surf. The higher the sea and the larger the waves, in their opinion the better the sport. (Ellis 1917, 278)

Surfing is reported to be among the favourite sports in Hawaii: „When playing in these places, each individual takes his board, and, pushing it before him, swims perhaps a quarter of a mile or more out to sea. The chiefs pride themselves much on excelling in some of the games of their country; hence Taumuarii, the late king of Tauai, was celebrated as the most expert swimmer in the surf, known in the islands“ (Ellis 1917, 279-280).

In other geographic regions, like North America, water sports are also common, such as among the Omaha: „There was one amusement in which both sexes of all ages, except infants, took great pleasure; this was swimming. […] Diving was practised by boys and girls and was enjoyed by men and women also. In these water sports the sexes did not mingle; women and girls kept together and apart from the men and boys“ (Fletcher & La Flesche 1911, 369-370).

Igbo children in Africa enjoy collecting objects thrown from steamers passing their village:

> When any article is thrown from the steamer, the little canoers at once plunge into the water and race madly for it. Meantime the empty canoes drift down-stream until the steamer is out of reach, when with lusty trudgeon strokes the owners overtake them. A youngster grasps by the stern and, by a series of vigorous fore and aft movements, swishes out the water and tumbles in once more. One has seen boys in their eagerness to pick up treasures swim right into the steamer's line of progress, and then, as the vessel appears to overwhelm them, laughingly fend themselves off along the vessel's side and disappear in the swirl and foam set up by the revolutions of the stern wheel. One naturally thinks that that must be the end of them, but presently their heads pop up again twenty or thirty yards astern, the black water babies having apparently quite enjoyed the extra excitement created by the steamer's wash. (Basden 1966, 134)

Sabine Kuegler, daughter of German missionaries who grew up among the Fayu tribe in West Papua, reported that children and adults liked to play with the clay at the shore of a river (Kuegler 2005, 178-179). She showed the Fayu children how to construct a chute with clay at the river. The Fayu children at first were sceptical, but then joined in with enthusiasm. They were completely covered with clay (Kuegler 2005, 133-134).

Thermoregulation

It is not entirely surprisingly that bathing seems to be linked to thermoregulation in hot climates. The Mundurucu in South America "bathe often—sometimes as much as five times a day—both to keep clean and to cool off from the tropical heat" (Burkhalter 2001, 76). A report about the Malays in Asia states that "every three or four houses have a well, where everyone bathes two or three times a day, more often in hot weather. I remember a woman saying to me one morning, that she had to get up and bathe three times during the previous night, which had been very hot" (Firth 1943, 13). Even in the normally cold Terra del Fuego in South America, „on very rare hot summer days a few men [Yahgan Indians] sometimes splash on the beach, without venturing more than two or three steps into the water. This is done primarily, however, to refresh oneself in an effort to withstand the unusual heat" (Gusinde 1961, 76). Similarly, the Copper Inuit of North America enjoy a bath on rare hot summer days: „Washing is unknown, and while a party occasionally bathes in a stream or lake on a very hot day, these occasions are few and far between" (Jenness 1923, 39).

Orlando and Claudio Villas Boas, Brazilian brothers and activists for the protection of indigenous populations in Brazil, reported from the Roncador-Xingu expedition, that on hot days, the Indians spent the day resting in hammocks, the shadows or in water (Villas Bôas & Villas Bôas 1994, 282). Member of the expedition liked to camp near rivers; bathing in the rivers in the evening was perceived as a very pleasant activity *("é o que pode haver de melhor"*) (Villas Bôas & Villas Bôas 1994, 423).

The Bagisu in Africa "sometimes washed their feet on a muddy day, but they never troubled to wash their bodies, though they might bathe if a stream or pool tempted them when the sun was hot" (Roscoe 1924, 5).

Ritual bathes and bathing taboos

Bathing and washing are often found in the form of ritual baths and bathing taboos within religious or cultural rituals in many cultures and in all geographic regions. As the present literature review does not focus on this topic, only a few examples are given.

One well known example of a ritual bath is the bath in the river Ganges in India, as Östör describes:

> Just as the ghat is prepared for the Goddess so the devotees have to prepare themselves for her. The devotees take baths to purify themselves for the Goddess. The water of the Ganges (Ganga, the sacred river, herself a Goddess) purifies, but any water taken from the open is Ganges water. Thus the water of lakes (bandh), temple tanks and rivers is proper for bathing men, ghats, and goddesses. Water from taps, wells, or puddles is not pure. Water washes away sins and faults (dos) knowingly or unwittingly committed, and is the best preparation for the arrival of the Goddess. Pure clothing, washed in an open body of water and dried in the air by the performers themselves, and pure garlands of flowers or of beads made from the fruit of sacred trees are to be worn after the bath. (Östör 1984, 77)

Ritual baths are common for specific life events as for instance childbirth, including ritual baths of the newborn child or of the young mother (the Belau in Oceania: (Barnett 1949, 102); the Lur in the Middle East: (Friedl 1997, 88); the Nuer in Africa: (Hutchinson 1980, 381-382)). Female initiation and the first menstruation are often accompanied by bathing taboos and ritual baths (the Tukano in South America: (Arnhem 1981, 75-76); the Yurok in North America: (Buckley 1982, 49); the Badaga in Asia: (Hockings 1980, 60, 62)). Also in marriage preparations ritual baths of both spouses are common (the Hopi in North America: (Voth 1912, 148-149); the Santal in Asia: (Skrefsrud 1994, 32); the Palestinians in the Middle East: (Moors 1995, 80)).

Ritual baths and bathing taboos are also known when a member of the society dies (the Bengali in Asia: (Fruzzetti 1992, 183); the Badaga in Asia: (Hockings 2001, 54, 57, 60); and the Otavalo Quichua in South America: (Parsons 1945, 119)).

Sometimes ritual baths or bathing taboos are linked to healing diseases (the Zulu in Africa: (Raum 1973, 221); the Trumai in South America: (Murphy & Quain 1955, 65)) or to the power of medicine men (the Orokaiva in Oceania: (Williams 1928, 32); the Yanoama in South America: (Wilbert 1995, 101)).

In most of the above-mentioned washing and bathing rituals a connection between physical and moral cleansing can be assumed, as this is a phenomenon widespread in many cultures and religions (Zhong & Liljenquist 2006).

Health problems caused by sea water

Bathing in salt water was repeatedly reported to negatively affect the skin. Anderson reports on the Tongans in Oceania in 1777, bathing in ponds: “They prefer these to the sea, though

most of them stink intolerably, because the water is a little fresher and they are so sensible that salt water hurts their skin that when necessity obliges them to bathe in the sea they have commonly some Cocoa nut shells of fresher water poured over them to wash it off“ (Anderson 1967, 932). Similar statements about Tongans were made by King on the same voyage (1967, 1365), by Koch (1978, 60) and by Mariner and Martin (1818, 292).

Dickson recorded that among the many problems of the Bedouin pearl divers in the Middle East „salt water, exposure to sun, and lack of fresh water to bathe in after diving all day, tend to produce sores and skin troubles“ (Dickson 1951, 485). The Garifuna children in Middle America were observed „bathing in the sea if the day is not too chilly and the sea not too rough; they rinse off the salt-water with fresh well-water“ (Hadel 1989, 51; see also Kerns 1983, 70). The Marshallese in Oceania „take fresh-water baths at least thrice a week; men who are in salt-water every day, fishing or canoeing, habitually baths in fresh-water before putting on dry clothes“ (Mason 1947, 80).

If fresh water is not available, plant oils or similar are used to deal with the problem of salt water. Müller reported on the Yapese in Oceania: „The cleanliness of the people of Yap is nothing remarkable in comparison with many Melanesian coastal peoples, although allegedly they bathe in the sea every day. Since they try to counteract the unpleasant effect of the salt water by rubbing with dry coconut meat and anointing the hair with coconut oil, all kinds of dirt immediately cling again to the skin, and in addition they often give off a rancid oily odor“ (Müller 1917, 57).

Aquatic predators

Predators like crocodiles or sharks can be a threat in water. Interestingly, aquatic predators do not seem to represent strong barriers to aquatic activities but can limit the propensity to enter water.

The Nuer in Africa, for instance, bath in rivers inhabited by crocodiles but limit the bath to a “hasty dip” (Evans-Prichard 1938, 75). When the Barundi in Africa cross rivers “there is much shouting to frighten away the crocodiles“ (Meyer 1956, 107). Meyer continued: „The lake dwellers learn how to swim (*kuoga*) when they are still children, but because of the crocodiles they do not go into the water very far. People seldom swim in the interior where the rivers have many crocodiles“ (Meyer 1956, 111). In Gambela in Ethiopia, children at the river Baro stay close to each other to keep crocodiles away (Bachem 1966, 67). Uhl reported

an interesting behaviour of two girls in the Central African Republic taking a bath in the river Lobaye. They were signing and hitting their hands on the water surface, in order to keep the crocodiles away (Uhl 1988, 114). A very similar behaviour was shown by Anyuaa children in Ethiopia taking a bath in a crocodile-infested river. They formed a column, holding each other's waist and kicking with the legs. At the same time they screamed and splashed the water. They were convinced that the crocodiles would perceive them as one large and dangerous organism and would not attack them (Leuenberger 1968, 188).

In South America, a similar threat is the caiman (Caimaninae):

> This reptile, which always lives in the water, comes out to rest and to sleep on the sands of the beaches and can be dangerous to [Warao] Indians and Creoles who are bathing in the river, since, when they are amusing themselves, playing and tumbling on the sand, the astute and clever cayman comes, selects the best game, and goes happily off with it under the water, to eat it later on the first beach that he comes to. The people of the Orinoco, who are very familiar with the astuteness of the cayman, of this ferocious reptile, make a little fence in the river, with stakes well driven in, in order to bathe; but there have been cases in the Río Grande where the cayman got inside the stakes and waited there for its innocent victim. (Turrado Moreno 1966, 179-180)

Wagley reports on the Tapirapé in South America:

> The safety of Tapirapé men depends upon the power of their shaman during the period each October and November when they must swim while they fish and shoot turtles; for in this region of Brazil rivers are infested with alligators, sting rays (Potamotrygon histrix), and the carnivorous fish called piranha (Serrasalminae). The Tapirapé also believe that large snakes lurk in deep pools of the rivers ready to wrap themselves around men and pull them beneath the water. During the year men will not swim in deep water unless it is absolutely necessary and they will fish only in shallow clear rapids. When they must swim to catch turtles, a shaman guarantees their safety. A powerful shaman dreams. He travels to the river, ties he jaws of the alligators with wires, strikes the piranha across their teeth so they cannot bite, and ties up the large snakes into knots with their own tails. (Wagley 1943, 75-76)

The Siriono in South America „in crossing deep rivers or streams, […] usually cover their genitals with one hand so as to protect them from the palometas which infest all of these waters. They also step with care so as to avoid sting rays, whose stabs leave nasty wounds" (Holmberg 1950, 43-44). Sabine Kuegler, a missionary's daughter who grew up among the

Fayu of Western Papua, reported from an incident at a river, where Sabine's family was bathing. When they invited the Fayu to join them, they refused, saying that this river was a crocodile river. When Sabine's father asked them why they did not warn him before, they answered that everybody knows that this is a crocodile river and that they were admiring the courage of the white family (Kuegler 2005, 174-175).

Sessile animals like shells can also be dangerous. Silas reported on the Trobriands in Oceania who collect pearl oysters:

> The small oysters are comparatively easy to get, but the larger ones involve the risk of encounters with marine creatures of which the shark is amongst the least terrible. The enormous rock cod is much to be feared. But worst of all is the giant clam, a tremendous shellfish sometimes measuring 8 ft. by 4 ft. and weighing possibly half a ton. The edges of the clam shells are as sharp as razors. They rest on the bed of a reef, almost invisible except for a dark snaky line marking the fluted lips that stand ready to snap at the incautious foot that treads upon them. One can battle with other monsters, but there is no escape from the grip of this terrible thing, short of hacking off the captured limb; and even then the scent of blood would bring sharks in hundreds to take what the clam had left. (Silas 1926, 126)

The Tiwi in Oceania also know several dangers in the sea: „When one considers that, together with sharks, these waters contain the large and dangerous salt-water crocodile and all manner of poisonous jellyfish, one realizes that to swim around in a high sea in the pitch dark requires considerable courage" (Goodale 1957, 12-13). The Hawaiians in Oceania learned how to deal with the danger of sharks:

> The only circumstance that ever mars their pleasure in this diversion is the approach of a shark. When this happens, though they sometimes fly in every direction, they frequently unite, set up a loud shout, and make so much splashing in the water, as to frighten him away. Their fear of them, however, is very great; and after a party return from this amusement, almost the first question they are asked is, "Were there any sharks?"" (Ellis 1917, 280)

A report by Thompson on the Lau Fijians stated that „men, women and children bathe daily in the lagoon, usually at sundown before the evening meal. This is done in spite of the danger of sharks which are common in these waters. Children are taught from babyhood to keep a keen lookout for their dark menacing forms, which are occasionally seen darting about in the lagoon right up to the shore line" (Thompson 1940, 15). Turner reported a similar behaviour

by the Samoans in Oceania: „At times their sport [diving from rocks into the sea] would be disturbed by an unwelcome intruder in the shape of a shark, but, unless it was the much-dreaded *Tanifa* [large dangerous shark], even this interruption failed to cause much alarm, but the cry of *O le Tanifa* was the signal for the whole party to beat a hasty retreat to the shore“ (Turner 1884, 140). One report about the Tongans in Oceania stated that “as a matter of fact there is no known instance of an Eueika man or woman having been injured by a shark, although both sexes freely and fearlessly swim long distances in the open sea“ (Collocott 1921, 238). Similar problems with sharks as described above are known for coastal cultures in North America, like the Yuki (Gifford 1965, 31) or the Pomo (Loeb 1926, 181).

5.4.3 Swimming

Swimming is reported regularly from all geographic regions (see Table 5.2). Oceania is the region where swimming is reported the most, and there is no report of a complete absence of swimming in this part of the world. Some cultures in Oceania were even described as “amphibious” by early explorers. An early example of an obvious exaggeration of the “amphibious status” of tribal people is supplied by Lapérouse. He reported on his travel to the Solomon Islands in 1785-1788 that the natives followed his ship by swimming one mile in the ocean (Lapérouse 1987, 47). He even wrote about having seen natives of the Easter Islands drinking sea water like albatrosses (p. 60). In his opinion, natives were as good swimmers as seals (p. 68). Very intriguing are the reports on the now extinct Agaiambu from the northeast coast of Papua New Guinea. Charles A.W. Monckton described an encounter with them which occurred in 1902 in his book *Some Experiences of a New Guinea Resident Magistrate* (Monckton 1921). According to Monckton, “’Ambu’ is the Binandere word for man, ‘Agai’ for duck; therefore the translation of the name ‘Agai Ambu’, which was used generally among the tribes, is the ‘duck- or web-footed people’” (Monckton 1921, 274). After stating that his description is the “only[74] authentic account that can ever be written, as they are now practically extinct” (Monckton 1921, 279), he wrote:

> Firstly, the true type of Agaiambu differed from other natives in these respects - I say advisedly the true type, because there were certain members of the tribe who nearly approached the ordinary type of Baruga native; but this was explained by the purchase of their mothers from the Baruga people. Placing an Agaiambu man alongside a Baruga native of the same height, one found that his hip joints were three or four inches lower than that of the

[74] This description was not the only one; see Walker’s report below.

> Baruga, one also found that his chest measurement was at least on an average three inches greater, while his chest expansion ran to as much again. The nostrils of the Agaiambu were twice the size of those of any native I have ever seen, they appeared to dilate and contract like those of a racehorse. Above the knee on the inside of the leg was a large mass of muscle; on the leg below the knee there was no calf whatsoever, but on the shin bone in front there was a protuberance of a sinewy nature. The knee joints were very wrinkly, with a scale-like appearance; the feet were as flat as pancakes, with practically no instep, and the toes long, flaccid, and straggling. Walking on hard ground or dry reeds, the Agaiambu moved with the hoppity gait of a cockatoo. Across the loins, instead of curving in fine lines as most natives do, there was a mass of corrugated skin and muscle. (Monckton 1921, 279)

Monckton discussed the possibility that several of Agaiambu's physical traits were adaptations to a semi-aquatic way of life:

> The skin of their feet was as tender as wet blotting-paper, and they bled freely as they crawled about upon the reeds and marshy ground of our camp. They had a slight epidermal growth between the toes, but nothing resembling webbing as alleged by the Baruga; the term "duck footed," therefore, had only meant tender footed, or, more literally, " water-bird footed." They were extraordinarily adept at handling their light, cranky canoes, and they were more at home in the water than any people I have either seen or heard of, and appeared to stand upright in that element without any perceptible effort; the one thing that my Mambare police feared, who were all very powerful swimmers, was entangling clinging water-weeds, but the Agaiambu would dive among them without the slightest fear. They told me they caught duck and water-fowl by squatting in a bunch of reeds, or covering their heads with water-weeds, until a flock settled near, whereupon they would dive under the flock and pull a bird or two under without disturbing the rest ; then, regaining their reeds or lump of weed, they would draw breath and repeat the performance. (Monckton 1921, 279-280)

The Agaiambu reported to Monckton that „they had once been a numerous tribe, but that about thirty years before some epidemic had swept through them and killed most of the people" (Monckton 1921, 279-280). Francis Winter, who also on one occasion went with Monckton to see the Agaiambu, gives the following account in an official dispatch to the Governor-General of Australia:

> The Ahgaiambo have for a period that extends beyond native traditions lived in this swamp. At one time they were fairly numerous, but a few years ago some epidemic reduced them to about forty. They never leave their morass, and the Baruga assured us that they are not able to

> walk properly on hard ground, and that their feet soon bleed if they try to do so. (Winter in Monckton 1921, 280-281)

In a report on an encounter with these people, H. W. Walker, Monckton's friend, described how an Agaiambu man tried to escape from two guides of the expedition:

> [He] plunged into the lake and disappeared under the tangled masses of water lilies. He remained under some time, but on his coming to the surface again, one of the Baruga men plunged in after him, and we witnessed an exciting wrestling match in the water. The Baruga man was by far the more powerful of the two, but he was no match for the almost amphibious Agai Ambu, who slipped away from his grasp like an eel, and swam away, with the Baruga man in close pursuit. (Walker 1909, 170-171)

He was impressed by the way how they walked: "They appeared to be slightly bowlegged and walk with a mincing gait, lifting their feet straight up, as if they were pulling them out of the mud" (Walker 1909, 173).

These reports are highly interesting and intriguing in the sense that this is the only case in the present review in which physical features of modern humans are interpreted as an adaptation to a semi-aquatic way of life. However, it is difficult to discern facts from fiction in these accounts. Even if it is the case that Agaiambu's physical traits were objectively described, it is difficult to distinguish genetic from environmental influences in the development of these features, as pointed out by Richards (1987, 203-204) in his comments of Monckton's report.

A further example of an early author stressing the amphibious nature of tribal people was reported by Chamberlain in 1906:

> With many savage and barbarous peoples all over the world children of both sexes learn to swim well at a very early age. The Andamanese boys and girls are very good swimmers, learning almost as soon as they can run; so also some of the Kootenay and other Indians of North America, who are very fond of the water. The Siouan Indians, according to Dr W J McGee (Ann. Rep. Bur. Ethno., XV, p. 172), were, for the most part, 'fine swimmers - men, women and children' - although they 'did not compare well with neighbouring tribes as makers and managers of water-craft.' Even among primitive peoples the best navigators are not always (perhaps not commonly) the best swimmers. The natives of Tahiti, and others islands in the South Pacific, 'are fond of the water, and lose all dread of it before they are old enough to know the danger'. Sir David Wedderburn (Ftn. Rev. XXVII. p. 801) describes the

> bathing of the Maoris of New Zealand, 'a nation of perfect swimmers, the women no less than the men', in the warm springs of the country: 'At sunset the whole population of a village, men, women and children, may be seen disporting themselves in the tepid depths, or seated, with the water up to their necks, on the smooth, enamelled sides of these natural termae. Infants in arms bathe along with the rest, learning to swim before they are able to walk'. We learn also that in the Maori legend, corresponding to the classic tale of Hero and Leander, it is the woman 'who performs the feat of swimming over to the island of Mokoia'. (Chamberlain 1906, 252-253)

Buck described the Samoan as trained "from infancy to cope with the watery element" (Buck 1930, 419). He continued:

> He paddles over sharp coral groves, swims over deep holes and channels, and dives round rocks and crevices. A strong wave that would dash a stranger against jagged rocks is avoided by falling forward over it when the place is shallow and submerging quickly under it when the depth permits. Even a novice under water would be swept against a sharp rock but the native fishers of either sex give a turn of the hand or foot and head into recesses and under projecting points with an ease that defies wave and current. The success that attends methods that another culture would regard as primitive depends on the high standard of skill attained in progression, both through and under the water, and in dealing with the various changes within the lagoon. People without this skill would starve amidst plenty. (Buck 1930, 419-420)

Similar accounts describe the Hawaiians: „There are perhaps no people more accustomed to the water than the islanders of the Pacific; they seem almost a race of amphibious beings. Familiar with the sea from their birth, they lose all dread of it, and seem nearly as much at home in the water as on dry land" (Ellis 1917, 278).

The Marquesans were even reported as not knowing that it is possible *not* to be able to swim:

> Marquesan children often learn to swim in shallow pools before they can walk. The natives are unable to imagine anyone being unable to swim. There have been cases in which whites were allowed to drown simply because it never occurred to the natives that the men couldn't swim and that the fuss the unfortunate whites were making was anything but a joke. (Linton 1939, 163)[75]

[75] Linton's statement should be considered with some caution, since signals of drowning are often not recognised by other persons (Barbeau 2011).

Similarly, Man attested to the indigenous Andamanese as being very good swimmers. He wrote:

> [In the Andamans] knowledge of the art of swimming is common to members of both sexes; the children even, learning almost as soon as they can run, speedily acquire great proficiency. In this accomplishment the Andamanese greatly surpass the majority of Europeans, but it is probable that, in competition with an experienced English swimmer, their best men would be distanced in the first few hundred yards, it being not so much for speed, as for the length of time they can remain in the water, that they are remarkable. (Man 1932, 47)

Ernst Haeckel described people of Malaysia as interacting regularly with water. Children and adults bath at least once, often several times daily. Children at the age of three or four are already proficient swimmers, preferring to play in water (Haeckel 1909, 230-231). Impressed by these patterns of water use, he wrote: "One might even call the Malaysians an amphibious race" (*eine amphibische Menschenrasse*) (Haeckel 1909, 231, my translation).

Swimming is also described in the case of the Igbo in Africa: „Swimming is one of the ordinary accomplishments of people living near the great waters; many are very proficient in the art, and are as happy in the water as out of it. The natives of some of the riverside towns seem perfectly fearless and plunge into the stream regardless of its state, whether in flood or otherwise" (Basden 1966, 134). The Bororo of South America were described „as much in their native element in the water as on the land" (Cook 1909, 361), and as „almost amphibious"(Cook 1909, 379). Similarly, the Warao of South America were reported to be very amphibious people by Turrado Moreno who wrote:

> [They are] born on the water and live and die on the water, they swim like ducks and dive wonderfully well. Men, women, boys, and girls know and learn the art of swimming masterfully, and they vary it in a thousand ways: they imitate dogs, ducks, birds, and animals, face up, face down, now on one side, then on the other, holding the foot with the hand, etc., for which reason they do not ordinarily run the risk of dying from drowning, unless it be down at the bars, where on certain days and at certain hours and times of the year, the waves swell, become rough, and rise almost to the sky, striking fear into the bravest. (Turrado Moreno 1966, 178-179)

A very interesting development concerning swimming ability can be observed in the Yahgan, a culture of Tierra del Fuego. Between 1918 and 1924, the Polish missionary Martin Gusinde

undertook four journeys to Tierra del Fuego to study the indigenous populations. He discovered that Yahgan men are not able to swim, but the Yahgan women regularly fastened their canoes a considerable distance from the beach and swam back and forth. With their canoes, the women collected sea urchins from the sea bottom, using a crab fork (Gusinde 1961, 260). When he asked a Yahgan man why he could not swim, this answered: „We don't have to learn it, for the woman takes us in the canoe to the beach and fetches us again from there“(Gusinde 1961, 371). Hyades also remarked on this curious difference in swimming skills between the sexes in the Yahgan. He reported that if a vessel would overturn, the men would drown while the women would swim to the shore. In answer to the question of why women could swim and men not, Hyades received the facetious answer from a man: only the women can swim because their breasts keep them on top of the water (*à cause des seins qui les soutiennent sur l'eau*) (Hyades & Deniker 1891, 213-214).

Different swimming strokes

Different swimming strokes are described in all geographic regions. Many show some similarities to the modern Western swimming styles. Water treading in a vertical position was described, for instance, among the Maori of Oceania when crossing rivers (Best 1924, 88-89). A kind of breast-stroke was described for the Maori (Best 1924, 88; Buck 1952, 240), and in the Andamanese in Asia "the 'frog-stroke' is the one in general use" (Man 1932, 48). In North America, a kind of breast-stroke is the common stroke in Chipewyan (Birket-Smith 1930, 72), the Yokuts (Spier 1978, 478), and, together with dog-paddle, for the Yuki (Foster 1944, 197-198). Gifford described the swimming style of the Yuki as follows: „They swam with both hands, belly down" (Gifford 1965, 68). Rattray described the Akan in Africa: „They swim either the ordinary breast stroke or a double overarm with a scissor-like kick of the legs" (Rattray 1923, 63).

A kind of dog-paddle was regularly reported. It is described in South America, such as with the above mentioned Yahgan women in Tierra del Fuego (Gusinde 1961, 372), or with the Siriono, described as excellent swimmers, able to swim a crawl stroke, as well as 'dog fashion' (Holmberg 1950, 43). The Warao, mentioned above, are also reported to know different swimming styles (Turrado Moreno 1966, 178).

In North America, the dog-paddle was described in the case of the Alutiiq: „They swam dog-fashion, although the fastest swimmer, a man named Angasha, who could keep up with a

three-man baidarka, used the European side stroke“ (Birket-Smith 1953, 104). Furthermore, dog-paddle was described in the Omaha (Fletcher & La Flesche 1911, 369), the already mentioned Yuki (Foster 1944, 197-198), the Cherokee (Gilbert 1978, 196), the Tlingit (Krause & Gunter 1956, 113), and the Quinault (Olson 1936, 134).

In Asia, the dog-paddle was described in use among the Iban in Borneo (Low & Roth 1892, 50) and also by the Okayama in Japan: „Children of any age are seldom allowed to go swimming, but most children of nine or ten have mastered a clumsy dog-paddle adequate to keep them afloat“ (Norbeck & Norbeck 1956, 663). In Oceania, the dog-paddle is the common swimming style as well as in Chuuk (Bollig 1967, 97), and is also used by the Santa Cruz Islanders:

> They swim with irregular movements, somewhat like dogs, and, strange to say, they often spread out their fingers when they push off. Perhaps it is because of their irregular, effortless movements that they have such extraordinary endurance. A boy of about eight swam under the 500-ton steamer of the Anglican Mission without ado. (Speiser 1961, 9)

Similarly, in Africa the Gikuyu were described using the dog-paddle (Routledge & Routledge 1910, 13).

Several swimming strokes described in use among tribal people show similarities to the Western crawl stroke. Such a stroke is known to, among others, the Maori in Oceania: „For a short, swift course he will use the overhand stroke (*kau tawhai*)“ (Best 1924, 88; Buck 1952, 240). The common crawl-like strokes seem to be used in Africa particularly, such as in the case of the Tanala in Madagascar (Linton 1933, 258). For the Dogon this style includes “alternately throwing the arms forward and then each foot one after the other after having bent the leg almost completely out of the water” (Griaule 1986, 101-102). Similarly, among the Barundi: „The swimming stroke is the same among all East African Negroes: with one arm far outstretched, the swimmer throws himself from one side to the other, striking out with only one arm at each stroke“ (Meyer 1956, 111). In the already mentioned Akan a “double overarm with a scissor-like kick of the legs” is used (Rattray 1923, 63).

In North America, crawl-like strokes were described among the Yokuts. Gayton, quoting another author, wrote that a swimmer in the San Joaquin “used a long overhand stroke“ (Gayton 1948b, 147), while in South America it is known to the already mentioned Siriono of

Bolivia (Holmberg 1950, 43). In Middle America it is known in the Taramuhara of Mexico: „In swimming they throw their arms ahead from one side to another“ (Lumholtz 1902, 238).

The back stroke and the side stroke were described only in the case of the Maori in Oceania (Best 1924, 88; Buck 1952, 240), and the Warao in South America (Turrado Moreno 1966, 178-179), while the scissor-like kick is known by the Akan in Africa, as already mentioned above (Rattray 1923, 63).

To summarize, the mostly frequently described swimming strokes in the present review were the dog-paddle (14 cultures in 5 geographic regions), followed by crawl-like strokes (8 cultures in 5 geographic regions), the breast-stroke (6 cultures in 4 regions), and in few cases back stroke, side stroke, scissor-kick or water-treading.

Learning to swim

An ancient account on the need to learn to swim in human is given by Lord Monboddo in his *Antient Metaphysics* (1779-1799) where he described that humans are not able to swim by nature, and that they have to teach their children to swim (Monboddo 1784, vol. 3, 73).

Detailed descriptions of teaching methods for swimming were reported for several geographic regions. In Africa, among the Tiv “in the vicinity of a river, some children are taught to swim. The proper method, Tiv say, is to lay them on the water, holding your hands under their stomachs and making them paddle. As they learn, you take your hands away. A few Tiv hold with the ‘throw them in’ school, but most say this is bad as the child comes to fear the water“ (Bohannan & Bohannan 1958, 381). A similar method is applied by the Abipon of South America: „ If the child be pretty big, it is thrown into the water, that it may learn to swim while it is but just beginning to walk“ (Dobrizhoffer 1822, 43-44). The Trobriand people in Oceania also teach their children to swim by a similar method:

> The native children are taught to swim from their earliest infancy. Some thirty miles from Samarai a white man was once walking along the beach, when he saw a native woman come down to the shore and deliberately throw a very young infant into the water. She stood quietly watching its struggles, and he, convinced that she was trying to drown her baby, ran to the spot. Before he could reach her, she calmly pulled the child out and returned to her hut. The next day the same thing happened. The woman was merely teaching her child to swim, the idea being that in deep water the infant will be kept afloat for a second or two and will instinctively strike out much as a dog would do in similar circumstances. (Silas 1926, 190)

According to experts, Herman Melville's first book, *Typee: A Peep at Polynesian Life* (first published 1846) contains both fiction as well as fact on baby swimming (E.Miller, Jr. 1973, 19). The following passage is traditionally quoted in books on 'baby swimming':

> One day, in company with Kory-Kory, I had repaired to the stream for the purpose of bathing, when I observed a woman sitting upon a rock in the midst of the current, and watching with the liveliest interest the gambols of something, which at first I took to be an uncommonly large species of frog that was sporting in the water near her. Attracted by the novelty of the sight, I waded towards the spot where she sat, and could hardly credit the evidence of my senses when I beheld a little infant, the period of whose birth could not have extended back many days, paddling about as if it had just risen to the surface, after being hatched into existence at the bottom. Occasionally the delighted parent reached out her hands towards it, when the little thing, uttering a faint cry, and striking out its tiny limbs, would sidle for the rock, and the next moment be clasped to its mother's bosom. This was repeated again and again, the baby remaining in the stream about a minute at a time. Once or twice it made wry faces at swallowing a mouthful of water, and choked a spluttered as if on the point of strangling. At such times, however, the mother snatched it up, and by a process scarcely to be mentioned obliged it to eject the fluid. (Melville 1932, 257)

According to Melville, this was not a single event:

> For several weeks afterwards I observed this woman bring her child down to the stream regularly every day, in the cool of the morning and evening, and treating it to a bath. No wonder that the South Sea Islanders are so amphibious a race, when they are thus launched into the water as soon as they see the light. I am convinced that it is as natural for a human being to swim as it is for a duck. And yet in civilized communities how many able-bodied individuals die, like so many drowning kittens, from the occurrence of the most trivial accidents! (Melville 1932, 257)

The similarity between Melville's and other reports, as for instance by Silas 1926 (quoted above) suggests that Melville's account might be based on facts.

Gusinde reported the swimming teaching method of the previously mentioned Yahgan in Tierra del Fuego:

> The mother teaches her daughter when she is still young. In a shallow inlet she rows her away from the shore, squats in the middle of the canoe, extends her outstretched arms over the upper edge and requests the girl to lie down on top of them, face downward; suddenly she draws her

> arms back and calls briefly: ‚Now swim!‘ The girl must now help herself until she has learned this art. Except for a few words of explanation, she receives no instruction. Sometimes during these exercises the mother places a flat stone on the girl's back. (Gusinde 1961, 372)

The Klamath in North America know several ways to learn how to swim:

> Another favorite activity of all Klamath children is swimming. Very young children are not allowed near the water, but by five or six years of age the child is paddling around in shallow water under the watchful eye of parents or of older children who help the younger ones to learn. The teacher holds the child around the waist and tells him to splash with his arms and legs. In other instances the child learns by himself or by verbal instructions. One informant related the following incident: ‚I thought I was swimming when I had my feet on the bottom. Someone laughed at me and said that wasn't swimming. He told me to kick my feet, too‘. (Pearsall 1950, 343b)

A detailed account of swimming teaching is reported by Ligers about the Bozo in Africa. The father teaches his son how to swim: he gives the son water from the bottom of the boat to drink, telling him that now that he has drunk the water from the boat he will float like a boat. In teaching the son, the father makes him go into the water up to chest level. The son swims to the shore, and back to the boat. The father gives him the rope of the boat and tells him that he should lie on the rope and make movements with the arms like the oars. The boy follows all the instructions and is happy to see how he can move in water. The father spends a considerable time with his son, and after 5-6 days the son can swim. After the boy can swim, the father teaches him how to dive: they dive in together to the bottom of the river and the boy learns to open his eyes. When they are at the bottom, the father counts the fingers of the boy in a very theatrical way, and when they count to five they come back; with time they count to ten. The father teaches him all the secret ways to stay longer under water. After all these procedures, the father teaches him how to catch fishes by diving.

The girls learn to swim from their mothers. The mother takes the girl with her to the river to wash clothes. While the mother is washing, the girl plays in the water. When the mother finishes the washing, she takes the girl a little away from the group. She tells the girl to lie on the water and to approach the mother by moving the arms and the legs. The girl tries to swim. The mother observes her and tells her to hit the water with the feet and with the hands. This they repeat for several days. In the evening the mother tells the father that the girl is learning to swim, and the father says that she has to drink the water from the boat. The girl will hear

this and will drink the water from the boat all day and then she tries to swim in the river. Sometimes she learns to swim on the same day, sometimes on the next day. At this point, the children organize a swimming game called *mpângava* (‘the current that encounters us’). All the children lie on the back on the water and hit the water with the feet and swim against the current (Ligers 1969, 18-19).

Sometimes accessories are used to teach children to swim. In the case of the Island Carib „the children in order to learn how to swim and become accustomed to the ocean waves, as well as to amuse themselves, lay on small planks. They let themselves drift against the breakers and are driven back into the mouth of a river“ (Breton 1958, 22). In the case of the Maori „children learned [to swim] early and were sometimes assisted with gourd floats (*poito hue*), the gourds being allowed to dry out without puncturing and then enclosed in netting“ (Buck 1952, 240). Similarly, with the Serbs in Europe „children exercise in their play and learn to swim with the help of gourds“ (Pavlovic 1973, 91). For the Amhara in Africa „during the first season, when they learn to swim, a rope is tied around the child's waist and held by an adolescent or young adult“ (Messing 1985, 209).

In several cases, learning by imitation was described. For the Nuu-Chah-Nulth in South America, children are taught to swim by other children, „either by direct teaching to display their superior wisdom, or perhaps by their own hesitant and less skilful performances which may have given their new playmates something approximating slow-motion demonstrations“ (Drucker 1951, 136). Imitation is reported to be important for the learning process for the Tiwi in Oceania: „Two important skills acquired early in this period are swimming and tree-climbing. I never saw anyone giving definite instruction in either skill, and it is probable that both are learned by imitation“ (Goodale 1971, 37). Similarly for the Manus in Oceania „[s]wimming is not taught: the small waders imitate their slightly older brothers and sisters, and after floundering about in waist-deep water begin to strike out for themselves“ (Mead 1930, 28), and the same applies to the Lepcha in Asia: „Jiroong can swim in the river in winter; he learnt from watching others and trying“ (Gorer & Hutton 1938, 429).

One curious system to get a baby used to water is to pour water into its nose. This method was described in an observation of the Igbo in Africa: “One of the objects of half choking the baby by pouring water into the nostrils, is to prepare it for the first sensations when learning to swim“ (Basden 1966, 63).

Alleged absence of swimming

The complete absence of swimming capability is described in 9 cultures (2 in Africa, 5 in North America, and 2 in South America). Again, most of the cultures described as not swimming at all live in cold or arid environments. For instance, Jenness reported on the Cupper Inuit in North America:

> Innocently devoid of clothes, I was disporting gaily in the water when the sound of voices made me look up. Men, women, and children lined the bank above me, intently watching the exhibition. None of them knew how to swim, or even that it was possible, and they gasped with admiration when I dived out of sight and reappeared a few yards away. Honi soit qui mal y pense. Ikpuck, The Runner, and even the latter's wife stripped off their clothes immediately and joined me in the water, eager to receive a first lesson in the newly discovered art. (Jenness 1959, 155)

A similar observation was made by Cole on the Aymara in South America:

> Most Aymaras follow the traditional practice of going barefoot so that they are always in immediate contact with the Earth. Their feeling for terra firma as the necessary base for all human operations is reflected in their inability to swim, even in the old times when Lake Poopo was in its glory. When they talk about the alien custom of swimming (or their own custom of drowning instead), one gets the impression that swimming seems almost as improbable to them as flying without an airplane does to us. In both cases, there is nothing there to hold one up. (Cole 1971, 38)

At the beginning of the 20th century, Lothrop reported that the Ona (living in Tierra del Fuego, where a very cold climate prevails) would not swim:

> Mr. William Bridges assured me that neither the Ona nor the Haush, to the best of his knowledge, had ever used a boat. In the summer of 1907 certain Indians were taken to Navarin island to tend sheep, and displayed great apprehension upon the waters of Beagle channel. No Ona could swim, and this tribe crossed swift rivers by forming a huddle so that any individual who stumbled would not fall and be drowned. Lacking all knowledge of navigation, unable to swim a stroke, and inherently afraid of deep water, how could the Foot Indians have crossed to Tierra del Fuego without the aid of others? (Lothrop 1928, 201)

However, as for bathing, many cultures develop swimming despite a cold climate, as we saw for instance in the Yahgan women of Tierra del Fuego.

One example of a culture in Africa reported as non-swimmers are the Maasai: „The Masaí neither can swim nor will learn to do so, and nothing on earth will induce them to go into water out of their depth. I have seen a fighting party of two hundred Masaí absolutely stopped by a deep channel in a ford not ten yards wide, whilst their adversaries on the opposite bank reviled them in true Homeric fashion“ (Routledge & Routledge 1910, 13). However, other Maasai populations more closely related to the Samburu were described as good swimmers (Huntingford 1953, 111), a fact that demonstrates that caution has to be exercised when interpreting historical reports. The Choctaws, living on the Mississippi River in North America, have been reported as non-swimmers, as well as the Tapuyas in Brazil (according to G. Brinton) (Chamberlain 1906, 252).

Drowning and water spirits

Drowning accidents are reported in many cultures, often from the ones described as unable to swim. Lindholm reported on the Pashtun in Asia: „Unfortunately, very few know how to swim, and drownings are common“ (Lindholm 1982, 11). However, in cultures known to for good swimmers, drowning accidents happen. In a Havasupai community in North America „the only known drowning of a Havasupai child occurred in an irrigation ditch in a neighboring white community“ (Smithson 1959, 47).

In several cultures a fear that small children were still unable to swim was described, even in cultures very fond of swimming. One example is the Tongan village Pangai in Oceania:

> Two or three other swimming-beaches lie within easy walking-distance. Yet young boys rarely learn to swim before the age of six or seven, and girls often much later. Younger children are often severely whipped for venturing to stroll unattended toward the nearest village beach. Yet the beach itself provides safe swimming at all tides. Elsewhere in Polynesia, by contrast, children of three are already fair swimmers and none, parents or children, seem to have that fear of the water which is characteristic of the Pangai villager. (Beaglehole & Beaglehole 1941, 66-67)

Similarly, among the Chuuk in Oceania „mothers particularly seem obsessed with the fear that their children will drown. This fear is not entirely groundless for the life histories contain several episodes in which this very nearly happened, although I know of no case in which a child actually died in this fashion“ (Gladwin & Sarason 1953, 82).

Often drowning is connected to the belief in evil water spirits. This is the case among the Tiwi of Oceania as children are rarely bathed, if at all, because there is a general fear of water and of the *maritji* [rainbow] spirits who live in the water, since these are said to be particularly dangerous to young children and pregnant women (Goodale 1971, 29). Among the Ute of North America there is a belief that „water babies" live in the rivers of the reservation. „Water babies" are described as being green-blue, having long black hair and long fingernails. Ute believe that these creatures can drown people, by pulling the unsuspecting swimmer under water (Jorgensen 1980, 429).

For the Okayama in Asia, Tanabata is, according to a legend borrowed from the Chinese, the day of the meeting of two separated lovers, represented by the stars Altair and Vega. Tanabata is said to be a good day for swimming in the sea, as it is a day when there are no "kappa". Kappa are mythical water creatures which lure horses and humans into the water to drown them (Norbeck 1954, 151). Hutchinson reported on rituals in Brazil in honour of the „Mother of Water". During the rituals, the fishermen go on the sea in their newly blessed canoes. Because their canoes were blessed by the priest, and because of the presence of the „Mother of Water", the men enter the water without fear. They jump in and out of the canoes and swim around them. This cannot be done at any other time of the year because it is considered dangerous to enter deep water (Hutchinson 1957, 161). The figure of „Mother of Water" is known under different names in several Middle and South American ex-colonies where African slaves have been brought (in Brazil, for instance, it is called Iara or Uiara or *mãe-d'água*). Some of these myths possibly come from the African „Mami Wata", a water spirit know in several West African countries that is said to make pranks like shaking boats, but also to kill people by drowning (Drewal 2008). In the central Niger delta, the Sorko have a particular water spirit cult:

> The belief in water spirits is found practically uniformly along the Niger, between Lake Débo and Bussa rapids. In the Eastern part of this section the cult is practised by water folk but more especially by the Sorko. It is believed that a spirit commands the life of the river, arranges currents and floods, and directs the movements of fish, crocodiles, and hippos. The spirit is said to be a woman with light skin and long hair. She is called dikko and holds the title harakoy or chief of the waters. A number of other water spirits assist her, such as the toru, dandu urama and zaberi. Originally the dikko and her kin formed an alliance with Faran Maka. The cult is especially prevalent among Sorko and the pagan Gungawa islanders who are

> considered the most devoted adherents. The Gungawa have adopted these Songhay rites and even retain the use of the Songhay names for the spirits e.g. Harakoy rather than the Hausa synonym Serkin Rua. Another aspect of the cult is the establishment of harakoy shrines along the riverside, consisting of a rectangular stone placed vertically in the ground. On these stones sacrifices are made, such as white chickens, milk, millet, porridge. These shrines are maintained by the Gungawa and other riverine groups, practically in every village on the banks and islands. (Sundström 1972, 112)

Accounts of water spirits are also used to keep children away from the water, in order to avoid drowning in children not yet able to swim, as for instance among the Chuuk in Oceania (Fischer 1950, 126). However, some authors believe that this fear of water can lead to poor swimming capabilities and therefore to a higher risk of drowning, as in the case of the Taiwan Hokkien in Asia:

> The understandable fears of these would-be immigrants were greatly multiplied by the intensity of fear of water common in China. Even the smallest bodies of water are believed to harbor murderous ghosts of past drowning victims (shui-kuei), each waiting to drown a new victim to replace it in its watery purgatory. Fear of water is instilled in children from infancy by anxious mothers. Consequently, few Chinese learn to swim, and the phobia becomes a self-fulfilling prophesy, drownings occurring with a frequency and under conditions suggesting that the slightest mishaps involving water produce instant panic and more evidence to confirm the prevalent conviction that immersion in water means certain death. (Sangren 1983, 325)

The Dogon in Africa believe in Nommo, a water spirit that can lead to drowning:

> Nommo is transformed, depending on the context, into a horse, a ram, a gleaming calabash or into a human being as a child, man, or especially a young girl. In this guise, he seduces the unwary and lures them into water, and at the call of the totem priest or the blacksmith their cadaver rises, nose and navel cut off. [Footnote 7: There are many stories in folklore about people who have drowned. Their spirits are said to be recognizable because they are ulcerous, dripping, and vomiting from water. The fear associated with drowning seems unjustifiably great given the small number of accidents (although we have no statistics). It may perhaps be explained by the fact that, since water is a life element, it seems inconceivable that an excessive amount of water could cause death.] Victims who do not die may become mad. This is why one is advised not to walk near water at night. The Dogon fear deep or turbulent water, and they are not fond, overall, of bathing or swimming in large bodies. (Calame-Griaule 1986, 499)

The fear of water spirits can lead to a refusal to help a drowning person. Blackman reports on an incident among the Fellahin in Africa, where a woman ventured in water on a hot day in order to take a bath. Suddenly she started to scream as she felt that she was drowning. “No one made any effort to save her, as they said that an „afrīt“ [soul?] of some drowned person had caught her by her hair and was dragging her down. They believed that if one of them attempted to save her he or she would probably be caught also - and, besides, the „afrīt“ wanted her and must have her!“ (Blackman 1927, 238). On the other hand, Ammar reports that saving a drowning person is regarded among the Fellahin as a noble act (Ammar 1954, 273).

Mangin reported on the Mossi in Africa, when they cross a river: „Woe to the man who dispenses with ferrymen, if he is not familiar with the bottom of the river and the strength of the current! He often drowns, and those whose aid he scorned do nothing to help him“ (Mangin 1959, 73). Similarly, the Ganda of Africa were reported as not helping a drowning person who had fallen in a river: „If a man was carried away by the current, his friends did not try to save him, for they feared that the river-spirit would take them also, if they helped the drowning man. They thought that the man's guardian spirit had left him to the mercy of the river-spirit, and in this way they accounted for his death“ (Roscoe 1911, 319).

Similarly in Asia, among the Taiwan Hokkien, drowning is connected to water spirits: „Besides the many drownings that resulted from capsized ferries in the old days, there have been several swimmers lost in more recent years. To the villagers these past drownings add immensely to the realistic dangers of the river since it is believed that the souls of those who drown must remain in the water as unhappy ghosts until they pull in another victim to take their place” (Wolf 1968, 15).

Some authors report on saving drowning people, like in a very early report on the Saami in Europe that is mixed with elements of legends:

> This Fellow having left his Habitation, to change it for a better, came with his whole Family to the Banks of the River Stoortutaad, which being frozen over, he endeavoured to pass it upon the Ice; but scarce had they reached the middle of it, when the Ice breaking under them, his Wife and another Woman were carried away by the swiftness of the Current; which the Laplander no sooner saw, but he plunged himself into the Water, Swum after them a great way under the Ice, and at last brought them both safe ashore, which so surprised some of his

> Country-men, that they were persuaded he had transformed himself into a Fish. (Scheffer 1704, 26-27)

Crossing rivers

Crossing rivers is done using different techniques, like swimming, wading, using floating devices to hold on or using rafts and boats. The opinion of how dangerous it is to cross a river is dependent not only on objective factors and swimming skills, but also from a subjective viewpoint. For instance, the German survival expert Rüdiger Nehberg described how a Yanoama man refused to cross a river with him in northwest Brazil, even with the help of a swimming belt (Nehberg 1983, 118-119). Nehberg quoted a missionary in Brazil, who commented that Brazilian Indians, even if they swim very well in local bodies of water, are extremely reluctant to take to water in other regions (Nehberg 1983, 118-119). This is especially true for Indians living far away from major rivers (Nehberg 1983, 109). In the case of the Abipones of South America „not only the men, but even very young women cross rivers without ford, bridge, or boat, by swimming“. To transport goods over the river, they use rafts which the swimmer holds (Dobrizhoffer 1822, 120). In the case of the Nambicuara of South America „canoes are unknown. Small waterways are crossed on a fallen tree; large ones by swimming, sometimes with the help of large floating bundles of burití palm stems“ (Lévi-Strauss 1948, 365). A similar technique was described by Alexander von Humboldt. He wrote how swimmers (usually young Indians) were used as postmen. The letters were transported in a turban-like cloth wrapped round the head. These swimmers often used a floating trunk under one arm as a help; the trip lasted two days over a distance of *ca* 96 km. Humboldt reported that this form of transport was used by several Indian groups living along the upper part of the Amazon River. He saw 30 to 40 Xivaro Indians (men, women and children) in the river arriving to the village Tomependa after such a trip (Humboldt 1859, 428-429).

The Yokuts in North America were also observed using floating devices to transport people or goods over a river. Gayton wrote:

> [E]veryone was a good swimmer, but children, sick persons, and goods sometimes had to be taken across the San Joaquin River, which is swift and deep. For this purpose there were large flat-bottomed baskets called te 'wıč (taskai', Gashowu). These were tightly coiled, but were not waterproofed. Infants and goods were placed in these and pushed ahead with one hand by one or two swimmers. A sick person would be laid on a raft of two or three logs; these too were

> used for goods, but baskets were preferred. Rafts also were pushed by swimmers; the river was too deep for poling. (Gayton 1948b, 155)

Fletcher described the Omaha of North America as good swimmers: “The current in the Missouri is always strong, so that it requires a good swimmer to make a safe passage across the stream. During the flood season the current is too rapid for anyone to venture to cross the river“ (Fletcher & La Flesche 1911, 369-379).

Some authors reported on people crossing dangerous rivers, as for instance in New Zealand:

> The Maori ever strove so to train young folk as to render them fearless in water, confident in their own powers to swim flooded rivers, and survive the perils of mishaps to canoes. The writer has seen some very remarkable performances by natives in the way of crossing raging floods in our swift and dangerous rivers, as when Tawera swam a twenty chain flood in the Land of Awa, and Eruera earned a £20 cheque by swimming the raging Whakatane to save stock on the left bank. (Best 1924, 92)

Shallow rivers are often crossed by wading, sometimes using sticks, as for instance in the case of the Barundi in Africa: „When reaching wide, open rivers, such as the Ruvuvu, Akanjaru, Luvironsa, and others, the traveller seeks out well-known fords and wades across, often up to his shoulders in water, and he uses a stick or a spear for support against the force of the stream. Everything that has to be kept dry must be carried in a bundle on the head“ (Meyer 1956, 219). Although boats, rafts and ships are not reviewed here, there are some cases in which humans used primitive forms of rafts or boats in which different degrees of bodily contact with water were observed. For instance, in simple rafts the boater has to sit in the water; this is described among the Guahibo in South America (Tyler 1929, 281); see also Lächler (1962, 208-211). Referring to Best’s account on Maori, Buck reports that „natives were expert in crossing swift or flooded streams in a slanting course with the current by treading water with the erect body half out of the water. Rivers were also crossed with the aid of a grip pole (*tuwhana*)“ (Buck 1952, 240). Crossing with the aid of floating devices are also known in Asia, as for instance among the Tibetans:

> Their hide rafts are also typical for this stage. The sheep or yak skins are removed in such a way that only the openings for the feet and head remain. These skins are tanned, the hair is removed from them, and they are well greased. The openings are tied shut, all except one, by which the skin is inflated. Four, six, or more skins are combined and covered with a lath to

> which they are fastened. A man is stationed at stem and stern to steer and paddle with an oar. These rafts are used not only to convey people but also to carry freight. An inflated sheepskin is used as water wings when a Tibetan wants to cross a stream without a raft. He lies on it with the upper part of his body and holds it in place with his arms. He rows with his legs. It requires a great deal of skill to keep oneself on the swimming bag. Before he inflates the bag the swimmer stuffs his clothes into it. (Hermanns 1956, 96)

In Africa „[t]hough neither a fishing nor a sea-faring people, the Zulus sometimes find it necessary, especially in the wet season, to devise some means of transporting goods across their rivers, and for this purpose they used to make a rough-and-ready kind of boat“ (Krige 1965, 215). In the case of the Mossi in Sudan, persons who wish to cross a river are helped by ferrymen: „The person who wishes to cross holds on to a thick beam, a gourd, or a simple clay jar, which holds him out of the water; sometimes two large sticks under his arms serve as a life belt. In a few places rafts are available, made of sticks connected with *séko* and covered with dry grass. The ferryman swims next to him and prevents him from being carried too far by the current“ (Mangin 1959, 73).

Gardi reported that the Buduma people in Bol, the Republic of Chad, Africa, often cannot swim. Since not enough papyrus rafts and no bridges or ferries are available, they transport their goods 800 metres over a sea-arm at Bol with the help of branches made from the light wood ambatch (*Aeschynomene elaphroxylon*) (see Fig. 5.1). He described how a woman undressed herself, lay down on her stomach on the primitive raft (*ca* 2 m long), stuck it between her legs, kept her head straight, sinking so far that only the head and shoulders were out of the water, and paddled merrily with the hands. She carried her clothes in a bundle on her head (Gardi 1957, 77).



Figure 5.1 Buduma women swimming with help of a raft constructed from Ambadsch wood. In the foreground a woman undresses herself, the raft on the water surface beside her. Behind her a second women with child is lying on a half-submerged raft. Photography by Gardi (1957, 32)

5.4.4 Diving and collecting food in water

Diving for recreation

Similar to swimming, the geographic region where diving is reported most is Oceania (see Table 5.2). One reason for diving is for play and competition. Von Kittlitz wrote on the natives of Ueai from the Woleai Region:

> [They] excelled even the other Caroline islanders in their diving ability; we saw some remarkable proofs of this during our short visit. One half-grown boy, who seemed about fifteen years old, often amazed us by the skill with which he could catch anything that we threw over board. We were anchored at a depth of nineteen fathoms, and he always managed to reach the object before it touched the bottom. He even succeeded in finding very small articles like pocket knives and other iron things, which we always showed him before tossing

> them into the water. Like a flash he jumped out of his canoe, which was on the other side of the launch; he swam under the keel of this boat and reappeared a few minutes later with the booty. (von Kittlitz 2009, 161-162)

In Africa, a very similar account was documented on the Igbo (Basden 1966, 134). Diving for recreational purposes is also described among the Dogon (Griaule 1986, 101). In North America, diving is described, among others, in the case of the Omaha: „Diving was practised by boys and girls and was enjoyed by men and women also“ (Fletcher & La Flesche 1911, 369). Among the Yuki „diving contests were won not by grace but by the ability to travel farthest under the surface. *U'nusilno'* (sulk under water) was a contest involving holding the breath under the water. To aid in these aquatic competitions, swimmers swallowed the air bags of suckers, which were supposed to impart to divers the characteristics of the fish“ (Foster 1944, 197). Similarly, among the Pomo „various kinds of diving contests were engaged in. A diving contest was called *lup'*. [...] Plunging, or seeking to see who could go the farthest, was called *camul diyan* (seeking to go). In high diving the man won who dived off the highest bank“ (Loeb 1926, 220). For the Quinault, “in diving matches the usual point was to see who could remain under longest” (Olson 1936, 134). In the case of the Havasupai „children dive under water to retrieve rocks, do handstands, race to catch a floating object, play touch-tag, strike upstream against a current where the stream narrows, swim under water, and strive at games and races which they devise“ (Smithson 1959, 48-49).

The Teguelche in South America „did a great deal of recreational swimming and diving, at which they were very proficient“ (Cooper 1946b, 157). The Warao, as already mentioned earlier, were described as “diving wonderfully well” (Turrado Moreno 1966, 178). In Asia, diving is described in several cultures, as for instance among the Andamans (Cipriani 1961, 485), the Garo (Sinha 1966, 20), and the Iban (Sutlive 1973, 311).

Fishing underwater and collecting sea food

The commonest reason for diving is fishing under water or collecting sea food (see video footage from a Baju fisherman during spear-fishing (Hugh-Jones 2011)). In the Maori culture “diving meant swimming downward and women were very expert from practice in gathering shell fish and crayfish by hand” (Buck 1952, 240). By contrast to the Tongans “diving (and spearfishing [*uku*]) is a quite productive fishing activity, but tends to be confined to younger men“ (Evans 2001, 107). For Hawaiians, spearfishing is carried out by men: “They crouched

sideways with one foot thrust out for support, with the spear (*la`au `o i`a*) held upward in the right hand—like a man shooting plover—and lunged with the spear and pierced whatever fish they chose, whether *uhu*, *ulua*, *kahala*, or some small fish" (Kamakau 1976, 86). Another interesting fishing method for the Hawaiians is eel fishing by hand:

> In snaring the eels the fingers were stretched wide apart while the thumb pressed down and held crabmeat in the palm of the hand. The back of the hand rested on pebbles, with the fingertips up against the face of the rock or of the crevice. The head of an eel would appear between the fingers as it came to eat from the palm of his hand. The fisherman would clamp his fingers together, and the head of the eel would be caught fast. If all the spaces between the fingers were filled, then six eels might be caught at one time. As their tails thrashed about, the fisherman would bite the eels in the middle of the back, and their wide open mouths would bite him on the cheek, on the neck, or on the ear lobes. (Kamakau 1976, 86-87)

Among the Ifaluk of the Central Carolines it is women's work to collect shellfish and crabs to eat. Crabs are eaten only if they are large enough (Burrows & Spiro 1957, 34-35, 102, 104, 157). The Ifaluk also hunt turtles (p. 102-103). The Marshallese know a large number of fishing and seafood-gathering techniques, each with an own name, depending on water depth, tools used, and species caught (Brower 1981, 76-77).

In South America the Bororo fish with nets directly in the water (Cook 1907, 56) and dive after fishes wounded with the arrow:

> When they cautiously approach the clear waters of a river and see a fish even with the water, they shoot it firmly, taking into account the deviation that the dart undergoes passing from the air to the water. Wounded, the fish flees, but the arrow that it carries in its body prevents it from submerging and reduces its speed. The Indian then abandons the bow and arrow and, holding an arago or a knife in the right hand, throws himself in the water and pursues the wounded fish, swimming with the left hand; upon approaching the fish, he wounds it anew or kills it immediately with arago blows. (Colbacchini & Albisetti 1996, 132)

The Tupinamba "when they do not have anything to fish with, they enter the water at night and upon feeling the fish catch them by hand; in the same way they get crayfish and shrimps from the bottom of the sea" (De Sousa 1970, 322). In the already described Yahgan of Tierra del Fuego „in exceptional cases the Indian woman jumps out of her canoe and dives down to get the sea urchin with her hands. […] She does this when she sees several animals next to

each other on the sea floor, which she cannot grasp with her crab fork because of the tangle of algae floating on top of it“ (Gusinde 1961, 260).

In North America, among the Yuki “diving after salmon in large pools and bringing them to the surface in the swimmer's hands showed aquatic proficiency, but was not a major method of providing food” (Foster 1944, 164). For the Yuki “sealions, common seals, and fur seals were caught and eaten. Young sealions sleeping on rocks were stalked and clubbed across the nose. A seal sleeping in the water might be taken by two or three swimmers, who seized it by the flippers and hit it on the nose with a stone” (Gifford 1965, 31). Gifford continued: “Mussels were also obtained from outlying flat rocks by men swimming to them with a basket attached to a stick” (p. 40). Gayton reported on the fishing culture of the Yokuts:

> Thirty-seven young men accompanied them, all of them [the chiefs] prepared with hand nets for catching fish in this San Gabriel River [copy of Nov. 19: Kings River]. This they did before my very eyes, with great agility, diving quickly and staying under the water so long that I prayed. Some remained under five credos [during five "Lord's prayers"], others no less than three [cinco Credos, y el que menos tres que yo reze]. (Gayton 1936, 78)

In another publication, Gayton reported on the same culture:

> Diving for fish was an indulgence of an able swimmer. Such a man (J.P. was said by all who knew him to be an expert at this) would swim down under water fifteen to twenty feet and seize an unwary fish in his hand. If possible a handful of sand was taken along or grabbed off the bottom to aid in holding the slippery fish, but an expert thrust his thumb under the gills. It took much practice to do this, and the skill is better regarded as a pleasurable stunt than as a fishing method. (Gayton 1948a, 76)

Lumholtz reported the following on the Taramuhara of Mexico in Middle America:

> During the night not one fish is taken up, but at daybreak the managers go down the river to investigate the effect of the poison, and upon their return the fish are gathered in, the men often diving into deep water for them. The work is done with great earnestness and almost in silence, the women helping the men in catching the fish. While the fishing is going on they do not eat any of the fish, for fear of not getting more, but during the day quantities are broiled and eaten, without salt or chile, however, and the bones are invariably thrown into the fire. Most of the fish are cut open in the back and placed on rocks or on trees to dry for future use.

> Such fishing may last for two days and nights, and is finished by dancing yumari and drinking maguey wine. (Lumholtz 1902, 403-404)

Itkonen described small boys from the Saami (indigenous people inhabiting northern Europe and the Kola Peninsula of Russia) fish assiduously in summer: “They sometimes catch fish with their bare hands from the hollows eroded into turfy brook-banks or in shallow ditches“ (Itkonen 1962, 844). The Iban in Asia „often catch the fish in the upper waters by diving into the rocky pools and pulling them out of the holes and crevices. The *scma* [possibly Banggai cardinalfish, *Pterapogon kaudernii*] especially are caught in this way“ (Low & Roth 1892, 50). Among the Andamans in Asia „the younger people delight in disporting themselves in the sea, and in displaying their skill in capturing a harpooned turtle or fish by diving after it“ (Man 1932, 48). Sabine Kuegler reported on how the Fayu in West Guinea described their former crocodile hunting technique. They dived under water to see if the crocodile had its eyes open or closed. When the eyes were closed they chained the legs of the crocodile and pulled the animal on land. Nowadays they hunt at night (Kuegler 2005, 188-189).

A study on maritime boat people in southeast Asia (the so called sea nomads or *Orang Laut*, including the Mawken and the Bajau) was published by Sopher (1965). These cultures live on boats and some of them avoid the land as often as they can, and are described as being extremely shy towards other people (1965, 131). According to Sopher they live from the sea, fishing and collecting seafood by diving in shallow coast waters. They have rather simple technologies, like spears and harpoons. They do not use nets, lines, traps or similar tools, a fact that characterises them (1965, 218). The most important method of food acquisition is gathering at the beach, and so they move from one strand collecting ground to another. They collect, among others, shellfish, crustaceans, turtles and turtle eggs (1965, 239).

Regular diving behaviour is described among the Korean (Hae-Nyo) (Hong & Rahn 1967; Hong 1965) and Japanese (Ama) breath-holding divers (Kita 1965; Nukada 1965; Teruoka 1932). The best known skin divers are the Ama of Japan. Although they may be male or female, most divers are females, and the word “Ama” is ordinarily applied to the female divers. Ancient references indicate that Ama “have existed for at least 2000 years” (Nukada 1965, 25). Ama are widely distributed along the shores in Japan (Birukawa 1965). They dive regularly during the summer months for shells and other seafood (Kita 1965; Maraini 1963; Nukada 1965). It is often stated that women dive more frequently than men because they have

more fat and can stay longer in cold water or stay longer underwater (see, e.g., Maraini 1963, 156). This statement – especially concerning the thermoregulatory effect of fat tissue in water – was also expressed in connection with pearl divers of the Tuamotu atoll in Oceania (Danielsson 1953, 220) and the Hae-Nyo, the diving women of Korea (Hong 1965; Rennie *et al.* 1962). However, other authors have pointed out the traditional aspects related to gender specific activities of the Ama (Nukada 1965, 26) and Haen-Nyo (Gwon 2005). Ama dive from the age of 15-16 years until 40-45 years. Young girls and elderly women dive at 2-3 m, close to the shore (Kita 1965, 50). Teenage girls dive 4-7 m in small groups starting from a boat. They use a net and a buoy to collect the shells; times after times they rest in the boat. This unassisted diving technique is called *cachido* (Kita 1965, 50). Expert divers use the so called *funado* technique to dive. The women descend rapidly with the help of weights 8-20 m deep, collect shells on the ground and are pulled up with a rope tight around their waist. Diving time varies between 40 seconds and one minute (Kita 1965, 50). Traditionally, the Ama use characteristic goggles with small leather or rubber balloons at the sides of the glasses, to allow pressure compensation during diving (Rahn 1965, 117-122). The Ama show physiological adaptations to diving, like a clearly larger vital capacity and maximum breathing capacity when compared to other Japanese women (Tatai & Tatai 1965, 81).

Among the Akan in Africa „the fisherman dives under the water, remains under from thirty to forty seconds, and comes up holding a fish between his teeth—to leave the hands free for swimming. I think they catch these fish possibly lying on the mud at the bottom, and 'tickle' them just as boys do in Scotland“ (Rattray 1923, 66). Randall Susman reported:

> The Mongo people we worked with in the 9 year bonobo study catch a lot of fish by hand. The men wade into streams and rivers and catch catfish and others by hand. The women dam small streams then collect plants and put them in the pools to poison or stun the fish. They let the plant compounds work in the water then return and collect the fish in the pools. (Randall Susman, pers. comm.)

Schapera reported on the Khoi in southern Africa:

> Fishing was also practised wherever possible, especially by the impoverished people. As tackle they used hooks of animal's teeth or of bone, nets knotted of bark fibre, basket traps of reed, and a pointed stick answering the purpose of a spear. At a later period their hooks were made of iron, and their lines twisted of animal sinews or catgut. They had no boats, but they

> were fearless swimmers and boldly threw themselves into the sea to reach a neighbouring rock, from which they fished with hook and line or harpooned the fish with their long wooden spears attached to a line. In rivers, creeks, or inlets they waded into the water to some distance from the bank, and when they saw a fish swimming within their reach pierced it with their pointed stick. Sometimes weirs were made in favourable situations along the shore, enclosing considerable spaces left nearly dry at low tide. In a similar way baskets were sometimes stretched across a stream in a shallow part. Men would stand behind these, while others waded up stream from a point below, driving the fish before them to the basket traps, where the men standing behind would then catch and throw them on the shore. (Schapera 1930, 304)

Sundström reported on the Bozo and Sorko of the Central Niger Delta:

> After the formal opening, men wade through the pool to spear crocodiles and other menaces to the fishing party. Thereafter the fishing party - men, women, and children, - form beating chains sweeping the length of the pond. They carry one triangular hand net in each hand, with which fish is scooped. These triangular nets, of different sizes, and spears are the typical fishing hand-tools of the Bozo and the Sorko fisherman. (Sundström 1972, 18-19)

And later Sundström continued:

> Traditionally harpoons and fish spears were the primary fishing implements of the Bozo, Sorko and the ancestors of the Nigerian Sorkawa, but it is only among the Sorko that these implements have retained this importance into present days. The classical, and possibly outdated, picture of the Sorko depicts an aquatic hunter with only a fleeting interest in fishing as such. Their exclusive way of life presupposes waters rich not only in fish but more especially in big games such as hippos, crocodiles and manatees. […] The most prized game of Sorko river hunters was the hippo. (Sundström 1972, 27)

Diodorus gave an early account on the "fish-eaters" (Ichthyophagi), a "group who inhabit the coast which extends from Carmania and Gedrosia (approximately modern south-eastern Persia and Baluchistan) to the farthest limits of the arm of the sea which is found at the Arabian Gulf" (Siculus 1946, book III, 15). According to Diodorus, these people lived almost entirely upon fishes. He wrote:

> They have their dwellings not far from the sea along the rocky shores, where there are not only deep valleys but also jagged ravines and very narrow channels which Nature has divided by means of winding side-branches. These branches being by their nature suited to their need, the natives close up the passages and outlets with heaps of great stones, and by means of these,

> as if with nets, they carry on the catching of the fish. For whenever the flood-tide of the sea sweeps violently over the land, which happens twice daily and usually about the third and ninth hour, the sea covers in its flood all the rocky shore and together with the huge and violent billow carries to the land an incredible multitude of fish of every kind, which at first remain along the coast, wandering in search of food among the sheltered spots and hollow places; but whenever the time of ebb comes, the water flows off little by little through the heaps of rocks and ravines, but the fish are left behind in the hollow places. At this moment the multitude of the natives with their children and women gather, as if at a single word of command, at the rocky shores. And the barbarians, dividing into several companies, rush in bands each to its respective place with a hideous shouting, as if they had come unexpectedly upon some prey. Thereupon the women and children, seizing the smaller fish which are near the shore, throw them on the land, and the men of bodily vigour lay hands upon the fish which are hard to overcome because of their size; for there are driven out of the deep creatures of enormous size, not only sea-scorpions and sea-eels and dog-fish, but also seals and many other kinds which are strange both in appearance and in name. These animals they subdue without the assistance of any skilful device of weapons but by piercing them through with sharp goathorns and by gashing them with the jagged rocks; for necessity teaches Nature everything, as Nature, in her own fashion, by seizing upon the opportunities which lie at hand adapts herself to their hoped-for utilization. (Siculus 1946, book III, 15)

Pearl diving and other commercial diving

In the case of the Belau in Oceania „[t]here are a few other products that are sold to the outside market. One of them is trocus [*Trochus*] shells. By regulation of the Palauan native government, the collection of this marine species is limited to one or two months during the year. During this limited interval, the young men spend most of their time collecting the animals on the reef or diving for them in the deep water beyond“ (Barnett 1949, 17). Pearl fishing is described in cultures of different geographic regions, as in the Trobriand peoples in Oceania (Austen 1945, 23; Silas 1926, 126), the Bedouin in the Middle East (Dickson 1951, 485) and the Saami in Europe (Itkonen 1962, 902-904).

Sometimes weights are used to aid diving in deep water. Bollig reports on the Chuuk: „To carry or lift floating objects or bring up heavy things from considerable depths (40 meters and more) is no trick for them. If a native wants to dive, he puts a stone on his shoulder so that he goes down all the quicker. When he arrives at the bottom, he throws the stone off again“ (Bollig 1967, 143-144).

In a detailed account on pearl divers of the Tuamotu atoll in Oceania the Swedish anthropologist Danielsson described a pearl fishing expedition (Danielsson 1953, 210-227). The natives reach diving spots on the island Takume with canoes. Mostly men dive for pearl shells, but some women join as well. According to the native men, women dive even better than them, because the greater amount of body fat would protect them from the cold and allow them to ascend quicker (p. 220). The pearl divers use almost no equipment, just metal glasses, a weight to descend, a glove for the right hand, and a belt with a net to locate the shells. They first dive in shallow water. They use the left hand to hold the corals and with the right hand they grab the shell and detach it from the wall (p. 217). The shells reach a weight of two kilos. After a while they dive in water deeper than thirty metres. At this depth they only descend with weights. They pull baskets to the ground which are then filled up and later pulled up, together with the weights (p. 218-219). The divers do not fill their lungs completely to dive. They remain under water between1 and 1,5 minutes (p. 219). Between dives they rest several minutes in the canoe. According to the natives, they could dive longer, but this would mean more resting time in between. They prefer a rhythm of one minute diving and few minutes in the canoe (p. 219). Elderly people and children clean the shells and look for pearls inside. The cleaning of the shells happens in the canoes and not in the villages for hygienic reasons (p. 220).

The negative effects of diving were reported among the Tuamotu (Cross 1965; Danielsson 1953). Accidents occur regularly in the form of cramps and vertigo and even pulmonary haemorrhage (*Blutsturz)* (Danielsson 1953). Several divers, especially beginners, die each season (Danielsson 1953, 221). Another danger is the giant clams (*Tridacna gigas*) and it is fatal for anyone who gets his foot trapped in one of them (p. 221). Also regularly described is the disease *Taravana*, a kind of decompression sickness known to Polynesian skin divers who dive repeatedly at great depth. The symptoms are vertigo, nausea, lethargy, paralysis and death. Danielsson observed another outcome of this disease: mental aberration (Cross 1965; Danielsson 1953, 223-224).

The negative effects of diving have also been described among the Tongans in Oceania:

> Tangitofuhia is used of the bleeding from nose and ears caused by staying a long time under water. In this place it seems rather to refer to a partial loss of consciousness resulting perhaps from striking the head or of staying under water too long, which renders the diver unable to

> find his way again to the surface. The unfortunate diver will swim about at random in his vain efforts to come up. Applied to one who wanders aimlessly about, or whose thoughts are erratic and disjointed (Collocott & Havea 1922, 112).

Evans reports from the same culture that: „in the long term diving is thought to sap the strength and health of those who do it“ (Evans 2001, 107).

The occupational diseases of the Ama have also been investigated. Harashima summarised his results as follows: “The chief type of diseases is chronic otitis media resulting in deformity or often rupture of the ear drum. Consequence of these changes is permanent loss of hearing capacity in various degrees” (Harashima 1965, 97). The diving syndrome *taravana* was also observed among the Ama (Cross 1965, 213).

5.5 Discussion: difference between humans and apes in behaviour towards water

The review on human interaction with water revealed that bathing and swimming are widespread among human populations in all geographic regions. In Oceania and parts of Asia aquatic activities are reported the most frequently, including cultures which show a high degree of exploitation of aquatic habitats, like the Amas in Japan or the Orang Laut in South East Asia. In humans, differences can be observed between the sexes or between adults and children in the extent to which the aquatic activities are shown. Humans develop several anti-predator strategies when faced with aquatic predators such as crocodiles or sharks, as for instance limiting the time spent in water, the depth reached in water or grouping and making noise by shouting and splashing the water surface.

Direct comparisons between humans and apes has to be carried out with caution, not only because of the role of culture in humans, but also because there is much less data on wild apes than on humans (Boesch 1998, 226). Nevertheless, a clear pattern is recognizable concerning the degree and regularity in which humans and apes interact with water: according to available data, clearly humans interact more intensively and more regularly with water than other extant hominoid species. While in apes aquatic activities are often observed in single individuals – for example, confirmed swimming and diving behaviour in apes is only known in two individuals in two species – in humans the described activities are mostly observed in several individuals of a specific culture. However, a broad variety in the readiness to take to water or in the reluctance to enter water is also present in apes – and this to a degree which

might surprise even some specialists. Under some circumstances single apes can show a strong affinity towards water, which seems to contradict the widespread view of these species as reluctant to enter water and unable to learn to swim. As discussed in chapter 4.3.6, this view is partially biased by data on patterns of water use in apes observed in captivity.

As expected, the exploitation of aquatic food resources was regularly observed in humans and to a much lesser degree in apes. Diving for food, although common in humans, was not observed in any ape. Tool use to access food in water (algae) was reported in wild chimpanzees (see "Feeding in or at water bodies" in chapter 4.3.3 and Table 4.2). Drinking behaviour using tools such as leaf sponges or leaf cups was observed in several apes (see chapter 4.3.3); tool-using related to drinking behaviour in different human cultures was not part of the present work.

During rain, apes sometimes use large leaves as "umbrellas". Both apes and humans seem to avoid rain if possible, but the behaviour is more nuanced in humans: as is well-known, human children often play in the rainfall, whereas this is unusual in young apes. A typical example of human behaviour towards rain is given for the Semang in Asia: "A brief rain storm passes over, but there is no close thunder or strong wind. The adults sit out the shower in their shelters, while the children play in the rain" (Endicott 1979, 21).[76]

One clear and expected difference between humans and apes is the constant behaviour of washing and bathing for hygienic purposes in humans, behaviour observed only in single captive apes, probably under human influence. Non-hominoid primates and apes wipe dirt from their fur, sometimes using tools (Shumaker *et al.* 2011, 100, 143). Extensive and deliberate diving behaviour for pleasure in apes was only observed in the captive chimpanzee Cooper, obviously a consequence of human influence, while this behaviour occurs regularly in many human cultures. Playing in water and thermoregulation are activities described in humans and in apes, with the already mentioned difference in degree of occurrence.

[76] There are several possible reasons why children show intensive play behaviour during rain. Beside the possibility to exploit the landscape in a different way - puddles on the street, sliding in mud (personal experiences as a child in South Brazil) – the visual, acoustic and tactile changes caused by the rain are certainly relevant; see also a remarkable video of a toddler allegedly experiencing rain for the first time https://www.youtube.com/watch?v=g_qMOCaLyv8, retrieved on 10th March 2014.

CHAPTER SIX – DISCUSSION AND CONCLUSION

6.1 Introduction

The aim of the present chapter is the discussion of some aspects of the complex interplay between available evidence for palaeoanthropological research and hypotheses proposed to interpret this evidence. The most important early and modern developments concerning reconstruction of the palaeoenvironment and anatomy of early hominins are analysed. Afterward, selected hypotheses proposed to contextualize early hominin evolution are presented in a table and analyse them from the point of view of the convergence approach, with special focus on water use in primates.

6.2 Summary of the historical roots of the savannah hypotheses

Research on the evolution of early hominins is experiencing a transitional phase, in which elements of earlier palaeoanthropological concepts are accommodated, refuted or replaced by new concepts. Indications of this transition can be detected in the 1960s (see below). However, prior to analyzing the more recent aspects of these events, it is important to understand the earlier development of the classical hypotheses contextualizing early hominin evolution (for a detailed analysis and references see Appendix D).

In brief, the first ideas about primeval man emerging in open plains within the framework of an evolutionary hypothesis were outlined in 1809 by the French naturalist Jean Baptiste de Lamarck in his *Philosophie zoologique* (Lamarck 2006 [1809], 170). Charles Darwin proposed two main hypotheses for the contextualization of primeval man: the island hypothesis (see Appendix D) and an intensely summarized version of Lamarck's scenario of primeval man leaving the forest and adapting to open plains (Darwin 1871, vol. 1, 140-141).

It seems that the picture of an arboreal ancestor of man abandoning the trees and adapting to open plains is an intuitive one, as it is strongly connected to the ancient dichotomy of non-human primates living in forests / humans living outside of forests. The terms "open plains", "savannah" or "open glades" in connection with human evolution was only used sporadically in the 19th century (Wallace 1889, 459) or early 20th century (Keith 1923; Weinert 1932, 209; Wells et al. 1931, 536). The alleged parsimony of open plains ideas (implied in direct passage from forest to open habitat) supplied the rationale for several concurring hypotheses addressing details of how early hominins interacted with this new environment. Dart is often

mentioned as the first author of the savannah hypotheses in historical introductions of palaeoanthropological publications. As shown in Appendix D, this assumption is incorrect: evolutionary scenarios containing elementary arguments of modern savannah hypotheses were regularly published before 1925, and fossil evidence found from 1924 onward was interpreted in the light of savannah ideas already known at the time.

For the first half of the 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 the contrast of forests as a place of stagnation and open plains as a place of development, and on the other hand the idea of "trees leaving the apes" instead of "the apes leaving the trees" as a consequence of climatic changes. These views influenced subsequent modified versions of the savannah hypotheses (see details in Appendix D). Characteristic for most savannah hypotheses formulated at this time (but also for some modern models – see below) is the tendency to conceive an oversimplified landscape where hypothetical human ancestors could exist and behave according to the premises of the specific hypotheses.

Parallel to climatic deterministic views, in the first half of the 20th century several authors proposed different models of early hominin evolution based on analogies between hominins and animals adapted to open environments (see Appendix D). The rationale for these comparisons 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 environment A and to adapt to an evolving 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. Among others, these models were based on analogies between humans and kangaroos, horses or first terrestrial vertebrates. In more recent investigations, the use of analogies has not disappeared, but was replaced by the use of baboons or social carnivores as referential models; see Table 6.2 for an overview of analogies proposed in palaeoanthropological discussion and references.

6.3 The interplay between fossil evidence and palaeoenvironmental hypotheses

6.3.1 From savannah to "complex environment"

Reviews of palaeoanthropological hypotheses often stress the role of modern palaeoenvironmental and anatomical studies in today's opinion on early hominins living not on savannah, but in a mosaic landscape. However, this opinion already had been expressed by several authors from the 1960's onwards. Boné (1960) reconstructed the australopithecine palaeoenvironment using mammal fossils and concluded that the emergence of hominins was connected to a mix of woody landscapes and open plains. Hemmer (1965) did a similar analysis concerning the environment of Pleistocene hominins, except australopithecines. He concluded that the typical hominin biotope seemed to consist of a wooded environment, loosened up by bush and grassland in the immediate proximity of water-places. Although few scientists would doubt that climatic history had a direct influence on human evolution, some authors in the late 1960s were not willing to accept simple assumptions on climatic changes and hominin evolution. One example is Anati's (1968) commentary on Emiliani's paper *The Pleistocene Epoch and the Evolution of Man* (1968). Anati believed that climatic changes should be considered as just one of many possible causes and probably not even the main cause in hominin evolution. This was a clear signal directed toward uncritical climatic determinism in the palaeoanthropological discussion, common in the past. Butzer observed that many interdisciplinary studies on prehistoric environments concentrated on the discussion of worldwide stratigraphic schemes and absolute chronology, rather than a full interpretation of the immediate environment of a fossil site during habitation (Butzer 1964, 7). In the 1970s he resumed his research on the palaeoenvironment in Africa, presenting a complex scenario of the earliest stages of hominin evolution, differing from the classical savannah hypotheses: "Thus we see that African australopithecines and the earliest hominines lived in a wide range of contexts from Ethiopia to South Africa: lakeshores, deltaic marshes, minor stream channels, river banks, upland sinkholes, and karstic fissures below valley floors or at the foot of escarpments" (Butzer 1977, 576). He concluded that the emergence of hominins during the late Tertiary and early Pleistocene took place mainly in relation to multiple interdigitating ecological opportunities (Butzer 1977, 577). As one of the first authors to challenge the climatic determinism of the savannah hypotheses, he wrote: "Although selective grazing by an increasing number of specialized ungulates appears to have favored the evolution of

grassland or savannah ecosystems during the Miocene, there is no basis for the now time-honored hypothesis that adaptive radiation was a response to progressive environmental change" (Butzer 1977, 577). According to Butzer, the evidence pointed strongly to mosaic evolution and ecological speciation of hominins; see also Rayner et al. (1993, 222) on Butzer's different views on the palaeoenvironmental reconstruction of Makapansgat sediments.

In the 1980s the concept of hominins evolving in open plains was still influential, but the idea of a more complex environment was sporadically mentioned as a complement to the savannah model. David R. Harris, the editor of *Human Ecology in Savannah Environments*, stressed the point that palaeoenvironmental data at this time allowed just a preliminary attempt to explain the origin of savannah (Harris 1980). In the same book, J. D. Clark supposed (in addition to some conventional views on savannah hypotheses) that the "fossil evidence and palaeogeography show that similar ranges of micro-environments existed then, as now, in the localities favored by the hominin populations, which appear to have exploited several of them regularly. These micro-environments included stream courses with gallery forest, lake plains, and grassland-forest ecotones" (Clark 1980, 41). He saw as evident that "it was within habitats consisting of mosaics of grassland, woodland, and forest that the hominin line first became differentiated from that of the pongids" (Clark 1980, 41-42). In a review of the book *Laetoli: A Pliocene Site in Northern Tanzania* (ed. by Leakey and Harris, 1987), Andrews concluded, from some faunal evidence presented in the book, that the hominin habitat in Laetoli "was more heavily wooded than any of the authors of this volume are prepared to acknowledge, and if there is any criticism that I would make of the book it is the uncritical acceptance of unspecified savanna habitat at Laetoli" (Andrews 1989, 180). In the same year, Cadman & Rayner (1989) published the results of their research on the sediments of the Makapansgat limeworks, and based on palynological evidence they concluded that the preferred habitat of *A. africanus* was forest or forest margin. A further reconstruction of the Makapansgat Valley when it was occupied by *A. africanus* (ca. 3.3-3.1 Ma) (Klein 2009), supported the existence of significant patches of sub-tropical forest and thick bush rather than savannah (Rayner et al. 1993). Some years later Bamford provided impressive results concerning the palaeoenvironments of Sterkfontein, in *Australopithecus* deposits, dated 2.6-2.8 Ma. She found fossil woods that have been identified as the liana *Dichapetalum cf. mombuttense*. Because today there is only one species of *Dichapetalum*, *D. cymosum* in South

Africa (a liana typical of central African gallery forests), she concluded that there must have been a dense, humid, forest-type vegetation at Sterkfontein during the Pliocene. Another fossil plant from the same site, the shrub *Anastrabe integerrima*, grows today on forest margins. This implies that rainfall was higher during the Pliocene, suggesting that gallery forests were widespread at that time instead of the grassland of today (Bamford 1999).

From Aramis in Ethiopia, where Tim White's team discovered remains of *Ardipithecus ramidus*, palaeobotanical and faunal evidence suggests a relatively closed, tree-dominated and well-watered habitat (White et al. 2009; White et al. 1994; WoldeGabriel et al. 1994). Stable isotope studies from the same place show that the shift to open and grassy environments occurred later than previously thought (as late as 1.7 Ma). There was little evidence of open savannah until after 1.0 Ma (Cerling 1991; Kingston et al. 1994). Spencer, who investigated metric data from cranial material of five African Plio-Pleistocene bovid taxa and reconstructed the diet and environment of these species, concluded that secondary grassland development was not related to the origin of the Homininae or to the evolution of bipedality in hominins (Spencer 1997). From Hadar, in Ethiopia, where *Australopithecus afarensis* was found, a mosaic of habitats including closed and open woodland, bush and grassland, was inferred from the fauna accompanying the hominin fossils (Johanson et al. 1982); see also Cerling et al. (2011).

In the 1980s many researchers became interested in the dramatic cooling that occurred between 2.0 and 2.4 Ma (Brain 1981; Grine 1985; Prentice & Denton 1988; Vrba 1980). As this period was obviously too late to be related to the origin of the first hominins, these and other climatic events were used to contextualize other critical phases in hominin evolution in the general framework of the most popular savannah hypotheses. The most important of these attempts were those of Elisabeth S. Vrba (1985a; 1985b; 1985c; 1995a; 1995b). She reviewed previous hypotheses on the interaction between environment and biotic evolution and concluded that “most hypotheses have offered no predictions of patterns of speciation and extinction events against the time scale” (Vrba 1985c, 235). In her own model (the turnover pulse hypothesis), Vrba tried to show a relationship between African bovid speciation and patterns of climatic change as represented by the oxygen isotope curves derived from deep sea drilling projects. Furthermore, she saw a similarity in timing between the emergence of the genus *Homo* and speciation amongst the bovids in Africa. She concluded that climatic changes were a primary (but not exclusive) factor in the speciation of hominins. Her specific

suggestion on the spread of savannah environments was similar to the classical views on the savannah hypotheses (1985a, 265). Vrba believed that "Hominidae were probably 'founder members' of the biota of the extensive African savanna, together with many other phylogenetic groups" (Vrba 1985b, 71); see also Turner and Wood (1993) and Turner (1995).

Tim White made a perceptive statement about the interpretation of palaeoenvironmental data. He stressed that even if specific evolutionary events in the history of hominins can be shown to correlate unequivocally with global climatic events, a causal connection should not be adopted without fully considering other faunal and floral elements (White 1985). However, retrospectively seen, the work of Vrba represented an important impulse for the empirical evaluation of the climatic forcing component of modern savannah hypotheses. In fact, at the end of the 1990s, many palaeoanthropologists began to refute systematically the exclusive climatic forcing models, trying to explain hominin evolution as "resulting from both climatic and intraspecific and interspecific competition" (Conroy 2005, 205). Many authors quoted in this discussion the Red Queen Model (Van Valen 1973), which does not predict a tight relationship between widespread climatic changes and speciation events. Some authors avoided assuming a specific environment to explain early hominin evolution (Potts 1998). Vrba's climatic forcing model was specifically challenged by the work of Foley (1994) and McKee (1994), who were not able to find statistically significant correlations between the first appearance of hominins and climatic changes. After an analysis of a large sample of fossil mammals from localities in the Turkana Basin of Kenya and Ethiopia, Behrensmeyer *et al.* (1997) came to other conclusions contradicting Vrba's ideas: "our data indicate that late Pliocene evolution in East Africa was affected by the cumulative ecological consequences of cooler, drier, and more variable climatic conditions rather than by a sudden change toward open habitats" (Behrensmeyer *et al.* 1997, 1593).

Important criticism of palaeoenvironmental reconstructions was influenced by research in other biological fields. Significant influence can be attributed to the work of Nikos Solounias and colleagues. In several papers they demonstrated that the traditional method of evaluating the palaeoecology of an extinct species was based on the assumption that the adaptations of this species were similar to those of closely related modern species. They observed that African savannah fauna species, because of their impressive diversity and beauty, invariably were selected as ideal models for interpreting many past communities. They noted that ungulate and carnivore faunas from Russia, Europe, India and the Indomalayan lands were

largely ignored. Solounias and collaborators pointed out that many of the earlier assumptions have been shown to be incorrect to some degree, and that this topic is much more complex than commonly believed. For instance, results of masticatory morphology suggest that many of the Pikermian ruminants are best approximated not by savannah species, but by those which inhabit Northern India, in the Park Kanha, a region that sustains a subtropical forest with vast glades and swampy lake margins (Solounias *et al.* 1999).

This and other analyses (Solounias et al. 1995; Solounias & Moelleken 1993; Solounias & Moelleken 1994) contradicted a widely held belief that fossil ungulates are evidence for the spread of savannahs over much of Eurasia during the Miocene, (the "savannah myth"). The results of a recent examination by microwear analysis on a large sample of the Pikermi and Samos ungulates show that "major dietary and morphologic ungulate evolution may take place within woodlands rather than as a consequence of species moving into savannahs both during the late Miocene of Pikermi and Samos and during the Pleistocene-Recent of Central Africa" (Solounias, Rivals and Semprebon, submitted). In several works Solounias argued that in using only fossils to reconstruct past environments, we often recreate the present environment of their modern descendants. In a popular contribution to current debates in the field, Richard Leakey and Roger Lewin pointed out a similar problem:

> The images we all have of the great plains of Africa, darkened by huge migrating herds, are indeed dramatic. So powerful are they that we tend to project them into the past, thinking that the landscape must always have been like that. Once again, it is all too easy to allow the power of present images to distort our pictures of the past. (Leakey & Lewin 1992, 85)

Indications of well-wooded to forest environments were found in connection with sites of two taxa supposed to be hominin: *Sahelanthropus tchadensis* at 6-7 Ma (Brunet *et al.* 2002) and *Orrorin tugenensis* at 6.1-5.7 Ma (Pickford 2006) (see also below). Inferences from palaeoecology and fossil fauna connected to *Australopithecus anamensis* (4.1-4.2 Ma according to (White *et al.* 2006)) indicate a mixed habitat, composed of dry, possibly open, wooded landscapes or bushland, including gallery forests (Leakey *et al.* 1995).

Thackeray and Reynolds (1997) rejected a scenario based on an oversimplified pattern of climatic change and speciation. They explored relationships between oxygen isotope ratios (as determined from analysis of foraminifera from deep-sea cores) and estimates of ungulate biomass, as determined from faunal assemblages from Plio-Pleistocene sites in southern

Africa (including the Sterkfontein Valley) using an approach outlined in Thackeray (1995). This analysis showed two different patterns: (a) relatively low ungulate biomass values can be associated with a relatively high degree of woodland and forest cover during periods between three and two million years ago; (b) higher ungulate biomass values can be associated with a greater degree of mixed grassland and savannah for later intervals. Therefore, they suggested that "episodic expansion and contraction of woodland habitats (occurring at intervals of less than 100,000 years) were of such short duration that speciation 'events' would not always be expected as a result of habitat fragmentation linked to climatic change over the African continent" (Thackeray 1995, 172). They believed that such fluctuations would allow a high genetic variability within lineages, such that boundaries between species and genera might be especially difficult to recognize. Thackeray and Dupont (2006) suggested that increased aridification and its associated changes in habitat were factors that contributed to the extinction of gracile australopithecines and the emergence of *A. robustus* in southern Africa.

Beside the climatic influences (Hornetz & Jätzold 2003, 28-38), other factors probably are more relevant in the formation of savannahs and grasslands. Tinley (1982) showed the extensive distribution of water-impermeable barriers at various depths in the ground in East Africa. These impermeable layers alter the soil's water balance, inhibiting the development of zonal forest vegetation. Walter and Breckle (2002, 16) pointed out the crucial influence of soil on this vegetation: "Savannas and grasslands are determined by the soil (edaphically) rather than by climate and are, therefore, to be regarded as pedobiomes". The work of Andrews and Bamford (2008) seized on this knowledge. They stressed that former methods of reconstructing extinct environments failed to take into account the range of habitat variability. They set up a new protocol for the reconstruction of palaeoenvironments relative to the fossil hominin site Laetoli, based on following premises: (a) habitat variability in the past was at least as great as at present; (b) variability at the landscape level is a function of variations in geology, soils, and topography rather than climate; (c) vegetation type at the landscape level can be reconstructed from these environmental variables.

The discussion on palaeoenvironment is still ongoing. Cerling and co-workers, for example, investigated hominin sites in the Awash and Omo-Turkana basins in eastern Africa using isotopic data from palaeosols. They concluded that in the majority of these sites open environments (less than 40 % woody cover) prevailed over the past six million years (Cerling *et al.* 2011). In his (mainly positive) commentary to Cerling *et al*., Feibel (2011) pointed out

that it is unclear if the soil carbonate proxy reflects accurately the temporal and spatial variability in the studied material. Feilbel stressed the difficulty faced in most attempts to associate fossil evidence to a certain environment: “Most of the fossils we have were found where an organism dies, or where its bones were transported to, and not necessarily where it lived” (Feibel 2011, 40).

6.3.2 Anatomical evidence of arboreal adaptations

Palaeoenvironmental and anatomical evidence is intrinsically related: researchers finding anatomical evidence for arboreal adaptation in a fossil hominin tend to search for a confirmation of wooded palaeoenvironment at this specific hominin site. In the 1980s, many scientists began to describe evidence for an arboreal type of locomotion in the australopithecines (Ashton 1981; Oxnard & Lisowski 1980; Prost 1980; Stern & Susman 1983). On the other hand, some authors (Latimer et al. 1987; Latimer & Lovejoy 1989) believed that arboreal behaviour (based on analysis of the calcaneus and talocrural joints) had become adaptively insignificant in *A. afarensis* and was totally eclipsed by the evidence for morphological specialization to terrestrial bipedalism. These results were compatible with Lovejoy’s conviction that hominins venturing into open habitats were already bipedal (Lovejoy 1981). In the same paper he related the further development of early hominins to variable and mosaic conditions resulting from climatic changes in the Miocene (Lovejoy 1981).

Lovejoy’s hypothesis was a direct consequence of developments in palaeoanthropology initiated some decades earlier (Hooton 1931, 114; Morton 1926; Munro 1897, 90-93; Osborn 1919, 82; Washburn 1951) and summarized in the sentence “hominins were first bipeds, the large brain and tool use came later”. In the first scientific meeting on hominin evolution held by the Institute of Human Origins in Berkeley, the debate over the foot of *A. afarensis* (and the footprints at Laetoli) was strongly polarized (Lewin 1983). White and Suwa suggested that non-modern aspects of the *A. afarensis* foot “may reflect emphasis on different aspects of bipedal locomotion than seen in *H. sapiens*” (1987, 513); on anatomical evidence for climbing in the shoulder of *A. afarensis* see Green and Alemseged (2012).

In 1994 four articulating hominin foot bones recovered from Sterkfontein Member 2 showed more human features in the hindfoot and more apelike traits in the forefoot of the fossil called “Little Foot” (Stw 573, probably a species of *Australopithecus* dated possibly as old as 3.5

Ma). The hallux of this fossil is appreciably medially diverged and strongly mobile, as in apes (Clarke & Tobias 1995); further descriptions of skeletal parts of Stw 573 are available (Clarke 2002; Clarke 2008). The interpretation of the anatomy of "Little Foot" supports the idea that tree-climbing was part of the life way of these early African hominins. Other strong evidence for an arboreal adaptation of *A. africanus* was supplied by the proximal (Stw 514a) and distal (Stw 514b) ends of a right hominin tibia, recovered from Sterkfontein Member 4 in 1989. They showed what seemed to be clear chimpanzee-like features, but specific details of the talo-crural articular surface and the close association of Stw 514 with large numbers of craniodentally-identified australopithecine fossils supported the view that Stw 514 is in fact a hominin tibia (Berger & Tobias 1996).

Between 1994 and 2002, four very early potential hominin species were described: *Sahelanthropus tchadensis* from Chad (ca. 6-7 Ma) (Brunet *et al.* 2002), *Orrorin tugenensis* from Kenya (ca. 6.1-5.7 Ma) (Senut *et al.* 2001), *Ardipithecus ramidus* from Middle Awash study area, Ethiopia (ca. 4.4 Ma) (White et al. 2009; White et al. 1994; White et al. 1995), and *Ar. kadabba* (ca. 5.8-5.2 Ma) (Haile-Selassie 2001; Haile-Selassie et al. 2004); see Fig. 6.1 and Table 6.1. Claims on the hominin status, locomotory anatomy and palaeoenvironments of these species are controversially debated (Harcourt-Smith & Aiello 2004; Harcourt-Smith 2007; Wood & Harrison 2011). For example, Sarmiento (2010) assumed that White and colleagues' classification of *Ar. ramidus* as an exclusive member of the human lineage post-African ape divergence (which is based on numerous dental, cranial, and postcranial traits) lacks sufficient support. White et al. (2010) replied that Sarmiento's conclusion that *Ar. ramidus* predates the human and African ape divergence is non-parsimonious. Following another argumentation, Wood and Harrison discussed the difficulties in recognizing accurately the hominin status of *Ardipithecus*, *Sahelanthropus* and *Orrorin*. Instead of assuming categorically that these species were not hominins, they stressed the possibility that some of the traits regarded as hominin in these species could also be interpreted as primitive hominid features or homoplasies (Wood & Harrison 2011).

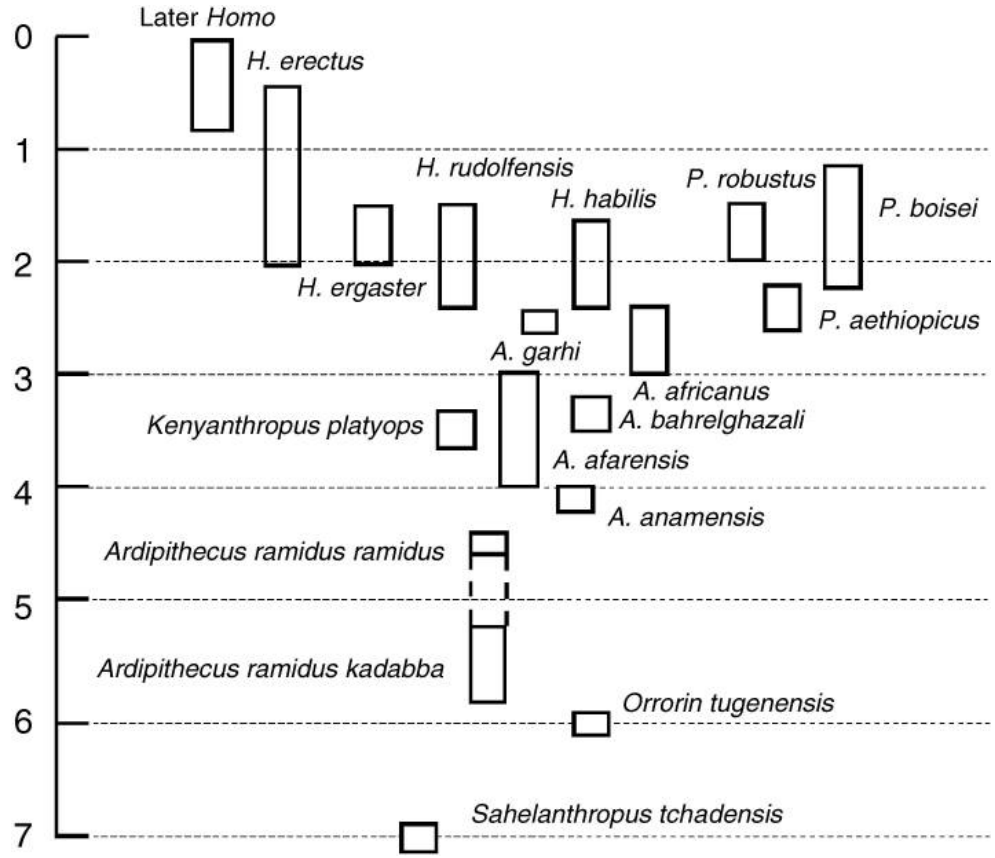


Figure 6.1 Temporal distribution of purported hominin taxa. From Harcourt-Smith and Aiello (2004).

Table 6.1 Extant hominoids and fossil hominines

Superfamily Hominoidea (hominoids)
Family Hylobatidae (hylobatids)
Genus *Hylobates*
Family Hominidae (hominids)
Subfamily Ponginae (pongines)
Genus *Pongo*
Subfamily Hominiae (hominines)
Tribe Gorillini (gorillins)
Genus *Gorilla*
Tribe Panini (panins)
Genus *Pan*
Tribe Hominini (hominins)
Genus *Australopithecus**
Genus *Kenyanthropus**
Genus *Paranthropus**
Genus *Homo*
Tribe *incertae sedis*
Genus *Ardipithecus*†
Genus *Orrorin*†
Genus *Sahelanthropus*†

Fossil hominines are shown in boldface. From Wood and Harrison (2011).
* These are almost certainly early hominins.
† These are purported early hominins.

The most important influence of the recent developments in palaeoanthropology can be summarized in a few sentences. The several indications of arboreal adaptations of early hominins forced a sensible modification of the scenario of early hominin evolution, pushing the hominins fairly close to forests or at least woodland environs. This interpretation connotates an evident contrast with the classical scenario defended until recently, in which the development of bipedalism was strongly tied to an expansion of grassland savannah. Whereas many hypotheses tried to integrate the new ideas in reformulated savannah hypotheses, some authors saw the new findings as reason to formulate alternative hypotheses based on the idea that the first steps in early hominin evolution took place in a forest environment. Different lines of evidence suggest that the last common ancestor of panins and hominins probably lived in the period between 8 and 4 Ma, and most probably between 6 and 4 Ma (Wood & Harrison 2011; Wood 2005). Although there is some consensus that the early hominins did

not develop in grassland savannah, there is no consensus about the context in which first hominins developed habitual bipedal gait (forest or a mosaic landscape).

A major point of debate in early hominin evolution concerns the question if knuckle walking evolved in the common ancestors of *Gorilla*, *Pan* and *Homo* and was retained in *Gorilla* and *Pan* or if the ancestor of *Gorilla*, *Pan* and *Homo* was a non-knuckle-walking generalized arboreal hominoid, so knuckle walking evolved twice, in *Gorilla* and *Pan*. It is remarkable that this question is still open so that the ancestral state of the last common ancestor of panins and hominins cannot be defined even concerning the most basic notions of their locomotory anatomy. It seems that *Ardipithecus ramidus* is a key species in the discussion on hominin phylogeny. If we agree with Wood and Harrison (2011), it is theoretically possible that *Ar. ramidus* is not a hominin, but evolved bipedalism convergently to hominins (or the traits interpreted as hominin in *Ar. ramidus* are not conclusive). Another kind of reasoning goes further. As shown in chapter 3 and Appendix C, convergences are very widespread in many taxa. Without molecular data, how precise can we be in recognizing that other fossils classified as hominins are indeed hominins and not hominoids which evolved bipedalism convergently under a similar selective pressure? Therefore, I suggest leaving this question open until more data are available about the selective pressure leading to hominin bipedalism. Because only humans are permanently bipedal among primates does not mean necessarily that this trait is unique.

6.4 Overview of hypotheses proposed to contextualize early hominin evolution

Selected hypotheses proposed to contextualize early hominin evolution will be analysed. For a better visualization and comparison of early and modern hypotheses on early hominin evolution, these models are presented in Tables 6.2- 6.5. It is obvious that the large amount of material will not allow the inclusion of several perspectives which are certainly relevant to understand hypotheses proposed to contextualize early hominin evolution, but which go beyond the aim of the present work. Especially relevant here is the use of (or lack thereof) arguments based on the idea that convergences can provide an important tool for the understanding of the functionality of organismic features. Basically, the table is an attempt to provide a representative sample of hypotheses on human evolution proposed before the consolidation of the modern evolutionary synthesis and a smaller, but still representative

sample of hypotheses, proposed after this time. Although priority was given on elaborated scientific hypotheses, some exceptions to these criteria exist. First, some of the sources refer to succinct statements (e.g., analogies between humans and desert animals), and are included because they reflect the strong influence of hypotheses proposing humans as well adapted to an arid environment – a typical element of savannah scenarios in human evolution. Second, some of the hypotheses can barely be considered scientific, for instance the so called primitivity hypotheses. The reasons for the inclusion of these ideas follow: the primitivity hypotheses are important both as background for the analyses of other hypotheses which are crucial to the topic of the present thesis (as explained in Appendix D) as well as for the strong relationship between the primitivity hypotheses and some influential concepts in early and modern palaeoanthropology (i.e., the idea of humans as basically non specialised creatures / as specialised in "not being specialised"). Furthermore, although clearly rejected by several influential palaeoanthropologists, the primitivity hypotheses were nevertheless rather popular in early anthropological discussion and played an important role in the anti-Darwinian movements in late 19th and the first half of the 20th century.

Hypotheses were grouped together when they shared crucial features. In several cases, hypotheses lumped in a group could be more precisely divided into different sub-groups. However, this task is anything but simple, since several authors changed elements of their hypotheses over the years. In some exceptional cases, contradictory statements concerning human evolution can be found within single works (see, e.g., Darwin's hypotheses, as discussed in Appendix D).

The evaluation of these hypotheses will consider the following aspects:

(a) How are the hypotheses related to other models proposed in palaeoanthropological literature concerning their main arguments and methodology?

(b) How did the hypotheses deal with relevant aspects of the proposed model? These aspects can be among others: (b1) the serious consideration of alternative ideas to the proposed hypotheses; (b2) the determination of precise information concerning important aspects of the proposed model, for instance the temporal and geographic placement relevant to the contextualization, or the sequence in which key features evolved; (b3) diligent analysis of the viability of the proposed theoretical model to explain early hominins living in a real environment.

(c) Are the arguments of these hypotheses based on the idea of convergence as a tool? If not, how did the authors justify the decision not to use a convergence approach?

(d) In the models using the idea of convergence as a tool: to what degree the use of convergence as a tool in evolutionary biology was reviewed in order to establish the methodology to be used in connection with the convergence approach? Furthermore, which criteria was used to establish which features to compare, which organisms to compare and how predictions can be formulated to allow further evaluation of the model?

Table 6.2 Hypotheses based on a savannah scenario

	Hypotheses, approaches or analogies	Main features considered (scenario)	Related hypotheses	Succinct description of the hypotheses	References
1.1	tower hypotheses / free hands hypotheses	bipedalism (open plains, mosaic habitat)	Basically, arguments from single savannah models were often implied in other savannah hypotheses. Specially related to the free hands hypotheses are 1.3, 1.4, 1.5, 1.9, 1.10 and 1.21	Evolution of bipedalism as a strategy to improve vigilance in open plains; "liberation" of hands for several purposes. Both sometimes part of the same explanatory framework	Lamarck (1994 [1809], vol. 1, 289-299); Darwin (1922 [1871], 78); Morris (1886); Munro (1897, 90-93); Reinhardt (1906, 7); Hoernes (1909, 141) ; Knauer (1916, 11); Osborn (1919, 60); Suschkin (1933); Washburn and DeVore (1961); Robinson (1963, 401; 1972, 257); Emiliani (1968); Heberer (1973, 34); Franzen (1972; 1973); Ravey (1978); bipedal posture provides a performance advantage for striking with the forelimbs: Carrier (2011)
1.2	tree-to-tree hypotheses	bipedalism (open plains, mosaic habitat)	See 1.1	Different scenarios explaining bipedal walking from tree-to-tree (or between tree groups)	Hoernes (1909, vol. 1, 215); Barrell (1917); Reinhardt (1906, 7); Huntington (1945, 26); Clark (1964, 187); Heberer (1973, 34)
1.3	dispersed food sources hypotheses	bipedalism (open plains, mosaic habitat)	See 1.1 Especially related are 1.2, 1.4 and 1.5	Evolution of bipedalism connected with locomotion between dispersed food sources	Rose (1984, 517); Sinclair (1986); Hunt (1994); Isbell and Young (1996); Sylvester and Kramer (2008); see also Mc Graw *et al*. (2005, 184)
1.4	carrying hypotheses	bipedalism (open plains, mosaic habitat)	See 1.1	Evolution of bipedalism connected with carrying food, tools, weapons, water, children, etc., sometimes with arguments about energetic cost of transport	Bartholomew and Birdsell (1953); Hewes (1961; 1964); Hockett and Ascher (1964); Washburn and DeVore (1961); Lovejoy (1981); Zihlman (1981); Laporte and Zihlman (1983); Stanley (1992); Tanner (1997, 204-205); Mayr (1998, 307); Watson *et al*. (2008)
1.5	feeding strategies hypotheses / home base hypotheses	bipedalism, social system (open plains, mosaic habitat)	See 1.1 Specially related is 1.3	Evolution of bipedalism connected with different feeding strategies, some making statements and predictions on the social organization, food sharing and complex communication of early hominins	Isaac (1978); Zihlmann & Tanner (1978); monogamous pair bonding, home base, reduced sexual dimorphism: Lovejoy (1981); Hill (1982); Blumenschine and Cavallo (1992); scavenging: Szalay (1975); Shipman (1986); Sinclair *et al.* (1986)
1.6	energy cost hypotheses	bipedalism (open plains,	See 1.1	Energetic advantages of terrestrial bipedalism (references include authors	Robinson *et al.* (1972); Rodman and McHenry (1980), Alexander (1991); Chaplin (1991); Steudel (1996); Leonard & Robertson (1997); Steudel-

	Hypotheses, approaches or analogies	Main features considered (scenario)	Related hypotheses	Succinct description of the hypotheses	References
		mosaic habitat)		defending different arguments)	Numbers (2003); Wang *et al*. (2004)
1.7	"fringe of the forest" hypothesis	not specified (fringe of the forest)	See 1.1	Emergence of early hominins in a fringe-habitat	using mountain gorillas as referential model: Livingstone (1962), inspired through ideas about edge-effects of environments on organisms by Audy (1957); this idea of first hominins developing in a fringe habitat is implied in several old and modern savannah hypotheses, as for instance in Steinmann (1908, 266) and Romer (1959, 327)
1.8	display hypotheses / appeasement hypotheses	bipedalism (open plains, mosaic habitat)	See 1.1	Bipedalism as part of threat display to defend against predators or as intraspecific appeasing signal or sexual display; as an additional explanation to the traditional savannah hypotheses	succint statement:Clark (1960); Livingstone (1962); Wescott (1967a, 738; 1967b); Guthrie (1970); Jablonski and Chaplin (1993)
1.9	throwing stones hypothesis	bipedalism (open plains, mosaic habitat)	See 1.1 Related to 1.10 concerning defence mechanism; related to 1.21 concerning hunting	Bipedalism evolving through throwing of stones as defence mechanism or to hunt small prey	hunting: Darwin (1922 [1871], 78); Müller (1894); Calvin (1982); defence: Darwin (1922 [1871], 78); Müller (1894); Fifer (1987)
1.10	thorny branches hypothesis	bipedalism (open plains, mosaic habitat)	See 1.1 Specially related is 1.9	Bipedalism evolving through the use of thorny branches as a possible defence mechanism against predators	Kortlandt (1980)
1.11	heat-adapted camel analogy	not specified (hot environment)	1.12	Succinct statement on human as „the most heat-adapted mammal, except possibly the camel"	Coon (1955, 259)
1.12	fat-storage analogy	fat tissue (not specified)	1.11	Succinct statement on adaptive similarity between the fat depot of women and the hump of camels or the fat of hibernators	hibernator: Hooton (1930) suggested this idea in an early work, but changed his opinion; hump of camels: Howells (1957, 102)
1.13	"cooling on savannah" hypotheses	hairlessness (open plains)	See 1.1 Implied in several savannah hypotheses, as for instance 1.14, 1.15 and 1.21	Hairlessness as a thermoregulatory adaptation to hot and dry savannah	Naef (1933, 161); Coon (1955, 267-268); discussed in a popular scientific book: Morris (1967, 46-48); Napier (1976); Ebling (1985, 39); Quigley (1971); contra in popular scientific books: Morgan (1972,

	Hypotheses, approaches or analogies	Main features considered (scenario)	Related hypotheses	Succinct description of the hypotheses	References
					16-17) (defending an aquatic hypothesis) and Ardrey (1976) (defending a sexual selection hypothesis); contra in peer-reviewed paper: Amaral (1996) (defending own ideas on hairlessness in a more forest environment)
1.14	later "cooling on savannah" hypothesis	hairlessness (open plains)	1.13	Australopithecines possessed a typical primate hair coat; hairlessness occurred only later, when *Homo* adapted to the dry steppe. It is also implied in some pictorial reconstructions of Australopithecines in the literature and museums. Strictly speaking it is an alternative to the classical 1.13	Geist (1978, 278-281)
1.15	sun-streamlined hypotheses	hairlessness (open plains)	See 1.1	Theoretical framework connecting bipedalism, hairlessness and several other features with thermoregulatory advantages	Wheeler (1984; 1985; 1990; 1991a; 1991b; 1991c; 1992a; 1992b; 1993; 1994a; 1994b; 1994c; 1996); Zihlman and Cohn (1988); Chaplin, Jablonski and Cable (1994); Sarmiento (1998); see also Chaplin *et al*. (1994); contra Amaral (1996)
1.16	radiator hypotheses	body proportions / large brain (open plains)	See 1.1	Changes in body proportions that favor heat dissipation only came with the evolution of the genus *Homo*/ network of veins acted as radiator to release thermal constrains on brain size in *Homo* (Falk)	McKee, Poirier & McGraw (2005, 183); Ruff (1991); Ruff and Walker (1993); Cachel (2006, 239-242); radiator brain hypothesis: Falk (Falk 1990)
1.17	marathon hypotheses	bipedalism (open plains)	See 1.1	Early hominins as adapted to run long distances in the heat (concerning first hominins and/or *Homo*)	Carrier (1984); Bortz (1985); Bramble and Lieberman (2004)
1.18	body weight hypothesis	not specified (open plains)	See 1.1	First hominins came down from the trees because their body weight increased; presented as an alternative to the savannah hypotheses, but very similar to these hypotheses	Hooton (1931, 114-116); Hennig (1929, 27); Weidenreich (1939, 87-88); Beurlen (1950, 417-418); Rensch (1972, 325); Henke and Rothe (1994, 345); contra Bergner (1965, 32)
1.19	savannah chimp	tool use	See 1.1	"Savannah chimpanzees" as model for early	Moore (1992; 1998); McGrew *et al*., (1981);

	Hypotheses, approaches or analogies	Main features considered (scenario)	Related hypotheses	Succinct description of the hypotheses	References
	model	(forest)		hominins	McBeath and McGrew (1982); Pruetz and Bertolani (2009)
1.20	horse analogy	not specified (open plains)	See 1.1	Superficial analogy horses / hominins to illustrate savannah hypotheses	Osborn (1927, 373)
1.21	"first terrestrial vertebrate" analogy	bipedalism (open plains)	See 1.1	Different scenarios explaining bipedal walking from tree-to-tree (or between tree groups) as analog to emergence of first terrestrial vertebrate (analogy explicit in Barrell)	Barrell (1917, 17); Reinhardt (1906, 7); Huntington (1945, 26); Clark (1964, 187); Heberer (1968, 34); see also Romer (1958), and references therein, who also defended hypotheses on the early development of tetrapod limbs as an adaptation for a water-dwelling animals living under drought conditions to shift from drying pools.
1.22	open plains primates analogies	bipedalism and other features (cliffs, open plains)	See 1.1	cliffs hypothesis: analogy between baboons / hominins, often suggesting that cliffs were used as refuge by hominins, sometimes suggesting that this environment was important for developing hunting and tool use	Müller (1894); Abel (1931b, 379-380; see also Ehrenberg 1949); Suschkin (1933); Ciochon and Corruccini (1976);
		bipedalism, dental anatomy (open plains)		seed-eaters hypotheses: evolution of bipedalism through a dietary specialization on small-object feeding (analog to sitting seed-eating papionin monkeys)	Jolly (1970; 2001); contra Szalay (1975)
		several features (open plains)		Other baboons analogies	Oakley (1960); Clark (1960, 312); Spuhler (1959); Washburn & DeVore (1961), but see Washburn (1978); DeVore & Hall (1965); Rose (1976); Wrangham (1980); Dunbar (1983); Sarmiento (1998)
1.23	social carnivores analogies	several features (open plains, mixed habitats)	See 1.1	Analogies between social carnivores and hominins	Read (1920); Dart (1953); Morris (1967, 19-40); Schaller and Lowther (1969); Ardrey (1970; 1974; 1976); King (1975); Hall (1977); Milton (1981); Poirier (1993, 48-71); Cachel (2006)

	Hypotheses, approaches or analogies	Main features considered (scenario)	Related hypotheses	Succinct description of the hypotheses	References
1.24	forest /open plains analogy; kangaroo analogy	bipedalism (open plains)	See 1.1	The assumption that animals living in open plains are further developed than forest-dwelling animals; the kangaroo was used as a specific example in this assumption	Hilzheimer (1921, 187)
1.25	singing hypothesis	bipedalism, hairlessness and other features (open plains)		Assuming that singing, body paining, long legs, head hair, hairlessness and clothes were used by hominins (early hominins? *Homo*?) as anti-predator strategy	Jordania (2011, 104-110)

Table 6.3 Alternative hypotheses to the traditional savannah hypotheses

	Hypotheses, approaches or analogies	Main features considered (scenario)	Related hypotheses	Succinct description of the hypotheses	References
2.1	gorilla analogy	not specified (fringe habitat)	1.1	First hominins evolved like mountain gorillas, adapting to a fringe-habitat	Livingstone (1962), inspired through ideas about edge-effects of environments on organisms by Audy (1957)
2.2	arboreal hypotheses	erect posture (arboreal habitat)		Erect posture and stretched legs on trees as preadaptation to terrestrial bipedalism	Stanford (2006); Thorpe *et al.* (2007)
2.3	island hypothesis	absence of natural weapons (large island)		Hypothesis suggesting that primeval man evolved in an island (in the absence of dangerous predators), proposed to explain the absence of natural weapons in human beings	Herschel (1831, 2); Darwin (1871, vol. 1, 157);similar idea on low selective pressure but without being specific about island: Klaatsch (1922, 47)
2.4	body weight hypothesis	not specified (open-plains)	See 1.1	First hominins came down from the trees because their body weight increased; it is on the one hand an alternative to the climatic determinism of classical savannah hypotheses, but otherwise similar to these models	Hooton (1931, 114-116); Hennig (1929, 27); Weidenreich (1939, 87-88); Beurlen (1950, 417-418); Rensch (1972, 325); Henke and Rothe (1994, 345); contra Bergner (1965, 32)
2.5	forest chimp	cognitive abilities, as		Forest chimpanzees as model for early hominins	Boesch & Boesch (1981; 1984); Poirier (1993,

	Hypotheses, approaches or analogies	Main features considered (scenario)	Related hypotheses	Succinct description of the hypotheses	References
	model	for instance the ability to make and use tools (forest)			48-71); Boesch-Achermann and Boesch (1994)

Table 6.4 Hypotheses stressing early hominins' interaction with water bodies

	Hypotheses, approaches or analogies	Main features considered (scenario)	Related hypotheses	Succinct description of the hypotheses	References
3.1	*Aquatile Hypothese*	bipedalism, hairlessness, swimming and diving behaviour, great amount of fat tissue, etc. (see Tables xx) (not specified semi-aquatic environment)	3.2	Hypothesis proposing the exploitation of a semi aquatic habitat as an essential factor in early hominin evolution; often with analogies between humans and aquatic organisms	Westenhöfer (1923; 1942)
3.2	aquatic hypothesis	almost identic with 3.1 (first conceived in connection with coast, later including also other water bodies)		almost identic with 3.1, but more specific on possible habitats. Darwinistic explanation of the adaptation.	Hardy (1960b); Morgan (1972; 1997); further elaboration of these ideas by Ellis (1986; 1991); Verhaegen (1997; 2002); Kuliukas (2002); scenarios including the exploitation of resources found in moist savannah and shallow-water habitats: Geist (1978, 215-217); Wrangham (2005), Wrangham et al. (2009); hypothesis combining savannah hypotheses with an aquatic scenario: Kraak (Kraak 1991);authors criticizing discussion on early hominin interaction with water bodies: Pickford (1991); Turner (1991); Leyhausen (1991); Pond (1991); Preuschoft & Preuschoft (1991); Langdon (1997; 2006); Jablonski (2006, 39-42); authors stressing the need of empirical

	Hypotheses, approaches or analogies	Main features considered (scenario)	Related hypotheses	Succinct description of the hypotheses	References
					investigations and scientific methodology concerning human interaction with bodies of water: Bender (1999); Bender-Oser (2004); Tobias (2002b; 2004); authors suggesting that a "shore-based" diet had a strong influence in human brain evolution: Crawford and Sinclair (1972); Crawford et al. (1999); Cunnane et al. (1993); Cunnane (1980); Broadhurst et al. (1998); Crawford (2010); Stewart (2010); authors suggesting that human diving reflex developed as an adaptation to diving behaviour in early hominin evolution: Schagatay (1991; 1996a; 1996b)
3.3	Amphibische Generalistentheorie	bipedalism and "generalized features" (semi-aquatic environment)	3.1 and 3.2	Hypothesis suggesting that humans evolved from a quadrupedal generalist ape in a semi-aquatic phase	Niemitz (2002; 2004)
3.4	Wading bonobo hypothesis (succint statements)	bipedalism and other features (watery and swampy environment)	3.2	Hypothesis proposed by De Waal suggesting that the special relation of *Pan paniscus* to water may have been more than marginally relevant during its evolution. De Waal mentioned among others bonobos' strong, long legs, referring to the aquatic hypothesis. The hypothesis was "written tongue in cheek". A similar idea concerning bipedalism was later proposed by Kortlandt: "The slender build, long legs and frequent bipedal gait of *Pan paniscus* might conceivably evolved as a secondary adaptation to the watery and swampy environment in the deltaic western part of the Zaïrean basin", without mentioning De Waal's idea.	De Waal (1993, 184-185); Kortlandt (1995, 25)

	Hypotheses, approaches or analogies	Main features considered (scenario)	Related hypotheses	Succinct description of the hypotheses	References
3.5	Aquarboreal hypothesis	Bipedalism, tail loss, air sacs (arboreal and aquatic environment)	3.2	Deviation of the classical AH, since it suggests that the hominoid common ancestor was already adapted to an aquatic environment. Hominoid specific features such as tail loss or air-sacs are explained as "aquarboreal" adaptations.	Verhaegen (Verhaegen et al. 2002; Verhaegen et al. 2011)

Table 6.5 Hypotheses which are not specific about the environmental contextualization

	Hypotheses, approaches or analogies	Main features considered (scenario)	Related hypotheses	Succinct description of the hypotheses	Authors
4.1	ectoparasites hypotheses	hairlessness		Reduction of body fur as adaptation to avoid ectoparasites	Belt (1874); Osborn (1926a, 7); Naef (1933, 161); Read (1920, 17); Rantala (1999; 2007); Pagel and Bodmer (2003); contra: Darwin (1882, 57)
4.2	sexual selection hypotheses	hairlessness		Reduction of body fur in response to sexual selection	Darwin (1922 [1871], 63);but see Hausschild (1926, 97); stressing the need of a physiological explanation for hairlessness: Burd (1986); Bartley (1994); Armelagos and Van Gerven (1980); contra: Morgan (1990, 59-68)
4.3	vestiary hypotheses	hairlessness		Reduction of body fur in response to the invention and use of clothes	succint: Hoernes (1909, vol. 1, 143); Matthew (1950, 42-43); Kushlan (1985)
4.4	heterochronic hypotheses	several human features, as for instance bipedalism, hairlessness, skin color, the form of the human skull	Some arguments of 4.4., 4.5, 4.6, 4.7 and 4.8 were sometimes shared	Several human features are not adaptive but neotenous characters	Bolk (1902; 1906; 1926); Schindewolf (1936, 46-65); Eiseley (1947); Montagu (1955, 14-16); Gould (1977); Vrba (1996). For a critical discussion see Slijper (1936); Schultz (1952); Starck (1962, 22); Dean & Wood (1984); McKinney & McNamara (1991, 291); Menke (2007)
4.5	specialized in "not	several locomotory	See 4.4	Many hominin features	Lorenz (1978, 260-268)

	Hypotheses, approaches or analogies	Main features considered (scenario)	Related hypotheses	Succinct description of the hypotheses	Authors
	being specialized" hypothesis	features		are expression of a low specialization	
4.6	self-domestication hypothesis	several features, as for instance hairlessness	See 4.4	Human beings are "self-domesticated" (in analogy with domestic animals)	Blumenbach (1806, 43) (succint statements); Fischer (1914); (1926); Hilzheimer (1927); Nachtsheim (1940); Lorenz (1940; 1959b)
4.7	deficiency hypothesis (*Mängelwesen*)	not specified	See 4.4	Human superiority is the result of an essential deficiency in many anatomical features	Suschkin (1933); Gehlen (1986 [1940], 33)
4.8	primitivity hypotheses	several features	See 4.4	Human beings evolve independently from other primates, even from other mammals	Snell (1887); Gaudry (1896); Klaatsch (1902; 1922); Stratz (1904); Kollmann (1905); Amegnino (1906); Wiedersheim (1908, 107, 126); Sergi (1913); Wilser (1910); Horst (1913); Knauer (1916); Osborn (1926a; 1926b; 1927; 1928; 1929); Westenhöfer (1923; 1926a; 1926b; 1934; 1942); Charles Hill-Tout (1921); Bolk (1926); Kleinschmidt (1926); Heilborn (1931); Adloff (1907); Giuffrida-Ruggeri (1902; 1921); Crookshank (1924); Dacqué (1924); Wood Jones (1918; 1948; 1929); Naef (1926a; 1926b; 1933); Quiring (1930); Šamberger (1933a; 1933b); Snoo (1942); Frietsche (1947); Kipp (1948); Hill (1950); Beurlen (1950); Kurtén (1973)

6.5 The evaluation of selected hypotheses on early hominin evolution using the convergence approach

A. Problems of hypotheses stressing alleged adaptive advantages in costly traits to perform functions which in other species can be fulfilled by a flexible functional focus

Several hypotheses on bipedalism assume an alleged advantage of a certain aspect of this postural and locomotor behaviour. A common problem in these hypotheses is related to the fact that the proposed functions (e.g., during vigilance, feeding, wading or transport objects) can often be fulfilled by several animals with a functional focus optimized in a long history of quadrupedal locomotory patterns.[77] Many species that regularly adopt a temporary bipedal posture have an anatomical predisposition for this behaviour, like carrying a large amount of the body weight on the hindlimbs or an increased joint mobility (as in primates). Meerkats (*Suricata suricatta*) use a bipedal posture for vigilance, similarly to bears (family Ursidae), marmots (genus *Mamota*), raccoon (*Procyon lotor*) and other rodents and primates. A further example of upright posture is observed in feeding on trees in the gerenuk (*Litocranius walleri*); following references treat the topic "bipedal posture" in humans and other organisms: (Bender 1999; Böker 1935, 146-154; Kummer 1965; Kummer 1991; Kummer 1975; Rose 1991; Slijper 1946). Most hypotheses stressing the advantages of hominin bipedalism lack convincing arguments as to why this form of locomotion is needed for a function which can be fulfilled by facultative bipedalism within real environments; see point (F) for hypotheses defending the advantage of obligate bipedalism in oversimplified envinronments and on habitual bipedalism-paradox.

B. Problems of hypotheses on adaptive traits without considering carefully the minimal precondition necessary to perform a given function (interlocking point)

For an explanation and examples of the interlocking point see chapter 3.3.2. For example, hypotheses assuming an energetic advantage of hominin bipedalism ignore (or treat stepmotherly) the fact that an energetically efficient bipedal gait would only begin to be

[77] However, several cases of bipedal gait are found in animals with long tails, which in some group are or heavy organs or tufted, used as counterweight and balance. This applies both to animals using a hopping locomotory pattern, as the kangaroos (Macropus), hopping mice (Notomys), kangaroo rats and kangaroo mice (Heteromyidae) and springhares (Pedetes), as well as to animal showing sustained running or walking, as in some extant reptiles like the common basilisk (*Basiliscus basiliscus*), or several extinct and extant archosaurs, like the genus *Struthiomimus* and birds (on upright stance in several aquatic birds see chapter 3.2.1).

efficient (if at all) when several anatomical traits associated to this locomotory behaviour are already optimized. This implies that the first stages in the evolution of these features cannot be selected for the function implied in the proposed hypothesis before reaching the interlocking point "optimized enough to be selected for an energetically efficient bipedalism". Such hypotheses should explain which other factors were relevant in the selective regime before the interlocking point was reached. Without this explanation, these hypotheses on hominin bipedalism have to be rejected as based on flawed arguments. A special aspect of this problem emerges if hypotheses are not transparent about the uncertainty concerning the temporal appearance of the considered trait. This applies, for example, to the fat-storage analogy (1.12), "cooling on savannah" hypotheses (1.13), sun-streamlined hypotheses (1.15 and chapter 3.4.3), several arguments of the aquatic hypotheses (Table 6.4) and the "singing hypothesis" which includes features like bipedalism, singing and hairlessness in the same context as the evolution of long legs and the use of clothes –features usually assumed to have evolved at clearly different stages in hominin evolution (1.25). The fact that the sun-streamlined hypothesis is often quoted in connection both with traits evolved in early hominins and at the same time with traits evolved in *Homo* species is a clear example of this problem.

C. Problems related to scenarios proposed as alternative to other models, but showing several basic similarities to the criticized model concerning methodology

As explained elsewhere (see chapter 2.4), scientists often use dichotomies to expose their own ideas. Sometimes these dichotomies are based on superficial elements of the discussed models with little or no discussion on the basic premises common to the proposed and criticized models. For example, some ideas were proposed addressing (real or imaginary) problems of other models, as in the "body-weight hypothesis" (1.18). However, several basic assumptions of the classical and body-weight hypotheses were very similar (as the initial stages of hominin evolution associated to an open environment). Similarly, the aquatic hypotheses defended by Alister Hardy and especially by Elaine Morgan stressed the differences between the aquatic model and the savannah model, without pointing out the similar methodological problems related to the use of convergence as a tool, characteristic for both scenarios (see Appendix D for explanation; see Tables 6.3 and 6.4).

D. Problems related to biological constellations and biological plausibility in the use of analogies

For an explanation and examples of biological constellations and biological plausibility see chapter 3.4. The use of biological constellations is related to different methodological problems and assumptions. Some analogies stress alleged adaptations in early hominins or *Homo sapiens* which lack any empirical evidence. For example, analogies between hominins and camels concerning an alleged heat adaptation in these species do not hold, as humans lose water at an extreme level in order to thermoregulate in hot environments – water loss through evaporation of sweat from the skin and due to insensible perspiration and moisture from breathing soon has to be replaced to prevent dramatically reduced performance or death (Parsons 2003). Other analogies are obviously flawed by stressing superficial, but not functionally related similarities between hominins (or apes) and other organisms, for example the analogy, camels / breasts (Table 6.2, hypotheses 1.12) and the analogies on "air sacs" in frogs and apes (see chapter 3.4.1) or based on an alleged similar environment responsible for the evolution of key traits in hominins and other organisms: as for example the analogy of hominins/horses (Table 6.2, hypotheses 1.20), the analogy of hominins/kangaroos (Table 6.2, hypotheses 1.24) and the analogy of hominins/baboons (Table 6.2, hypotheses 1.22) and several comparisons of the aquatic hypotheses where traits of fully aquatic mammals were compared with early hominins (see several models listed in Table 6.4). Finally, some analogies referred to an alleged similarity in the general evolutionary process, as in the case of the analogy to hominins/first terrestrial vertebrates (Table 6.2, hypotheses 1.21).

This similarity does not imply that both models are similarly parsimonious, but rather the similarity in the attempts to present complex evolutionary events in oversimplified schemas based on climatic deterministic models and "didactic scenarios". The analogy of hominins/horses illustrates well the pitfalls of superficial comparisons. According to traditional hypotheses, horses (family Equidae) primarily emerged as browsers adapted to open terrain; the context in which Equidae evolved seems to be more complex than once believed (MacFadden 1994; Mihlbachler et al. 2011; Solounias et al. 2010). In contrast to early analogies, there are no similarities between horses and humans in the sense of convergent features as adaptive responses to grassland savannahs. As explained in Appendix D, the analogies horse/humans were motivated by the excellent fossil record of early horses in the late 19th century and the popular picture of horses as "noble" animals – some scientists

could not resist the temptation to compare this material with the then available scarce hominin fossil evidence and to use this comparison to make inferences on human evolution. Interestingly, horses are not unique in terms of their specific adaptation to open landscapes: some extinct South American litopterns, like the proterotheriids, showed a trend toward limb elongation and side-toe reduction that are remarkably convergent to the adaptions of limbs in horses. *Thoatherium*, for example, were even more specialized than Equidae concerning cursorial adaptations – it had only one toe on each foot and no vestiges of side toes, as found in modern horses (Matthew 1913, 32ff.; Prothero & Schoch 2002, 13-14, 215-216; Thenius 1979, 217-218).

E. Problems related to lack of data concerning crucial issues in palaeoanthropology

We do not know the precise selective regime mediating the emergence of terrestrial bipedal gait in the basal hominins. Students of human evolution are defending various views on the contextualization of early hominins, and the fossil data introduced in the last two decades has opened more questions than answers. For example, we still do not now when certain soft tissue evolved in hominins, like hairlessness or a great amount of subcutaneous fat tissue (see references in chapter 6.8.1). As part of the same problem, we do not know if hairlessness and an increased amount of subcutaneous fat in hominins emerged at the same time and under equivalent selective pressures. It is remarkable how this evident aspect is often not explicitly stated in hypotheses proposing explanations for the emergence of these traits. There are some preliminary genetic investigations focusing on the topic hairlessness. Genetic differences between humans and chimpanzees/gorillas in hair genes, for instance, the inactivation of the human *hHaA* gene, indicates that hominins might have lost their hair cover less than 240,000 years ago (Winter et al 2001). The switch of pubic lice from gorillas to hominins 3-4 million years ago suggests that pubic hair, but not body hair and therefore hairlessness, was already present in hominins by this time (Reed et al 2007). Genetic variation at the *MC1R* locus leading to stronger skin pigmentation was interpreted as an indicator for the beginning of hairlessness 1.2 million years ago (Rogers et al 2004). These examples show how difficult it is to establish from indirect evidence when body hair was reduced in the hominin lineage, whatever the functional focus was.

Additionally, as already mentioned by Dawkins, the tail loss topic in apes “is a subject that biologists discuss surprisingly little” (Dawkins 2004, 127) – a surprising fact because of this

trait's importance to the interpretation of hominoid evolution. The same applies to tail loss in mammals. There is a poster on the subject (MacKenzie & Begun 2009) and the authors have planned a paper on it (MacKenzie, pers. comm.), but as yet it is not published. Lack of data is also a problem in several topics connected to water use in primates. Generally speaking, data on swimming and diving behaviour in terrestrial organisms (see a short summary in chapter 4.2.6) is rather sparse when compared with the investigations carried out on these behaviours in aquatic organisms.

F. Problems related to contextualize human evolution in an oversimplified environment

The process of constructing and analysing optimization models was described as "among the most drastic simplifications tolerated anywhere in biology" (Seger & Stubblefield 1996, 118). An even stronger oversimplification is implied in influential palaeoanthropological hypotheses. (To be sure, simplification is a normal and necessary aspect of scientific hypotheses, but sometimes the degree of simplification reaches a level that leads to a distortion of reality.)[78] An interesting example is related to the word "savannah". Although some specialists pointed out the ambiguity of the concept "savannah" (Harris 1980), in the long history of the open plains models this ambiguity usually was not regarded as an obstacle. Rather the opposite is true: this ambiguity favoured the contextualization of early hominins in the dissimilar habitats (from forest or forest fringes to open grassland) which were subsumed under the umbrella term "savannah" (see Appendix D). In a recent attempt to reanimate the concept of the savannah hypotheses (Domínguez-Rodrigo 2014), the ambiguity of the term "savannah" was explicitly discussed but not eliminated. As pointed out by White (2014) in his comment on Domínguez-Rodrigo's paper. Domínguez-Rodrigo referred to the historical roots of the savannah hypotheses without considering previous extensive historical investigations on this topic (Bender *et al.* 2012).

One of the most interesting examples of an oversimplified scenario where hypothetical human ancestors could exist and behave according to the premises of the specific hypotheses is Wheeler's sun-streamlined hypothesis (see chapter 3.4.3). As early as 1966, Underwood and

[78] For an investigation of different forms of simplicity in sciences see Bunge (1963). In the preface of his *Brave New World Revisited*, Aldous Huxley aptly summarized the problems associated to simplifications in a single, famous sentence: "Omission and simplification help us to understand – but help us, in many cases, to understand the wrong thing; for our comprehension may be only of the abbreviator's neatly formulated notions, not of the vast, ramifying reality from which these notions have been so arbitrarily abstracted" (Huxley 2004, xxi).

Ward showed that a vertical posture in humans increases surface area available for warming when the sun is low (morning and evening) and minimizes heat load during midday. However, they did not propose a sun-streamlined hypothesis, as they were aware (as shown in Fig. 6.2) that humans adopt various postures when exposed to the sun's rays (Underwood & Ward 1966). Mobile living organisms are difficult to analyse with static thermal models, especially if these organisms are constantly changing posture during foraging in a way that does not indicate an association with the position of the sun. Considerations of strategies to reduce heat stress using thermal models are feasible when the analysed object is static, as in the case of human architecture (Givoni 1992) or animal architecture (see chapter 3.4.3 on the nest of compass termites), or when postural behaviour is clearly associated with the direction of the sun's rays; see chapter 3.4.3 on examples concerning the Cape ground squirrel (*Xerus inaurs*) and the obelisk posture in dragonflies (Libellulidae). This does not apply to humans, as they are obviously not static elements in open plains – they prefer to avoid heat stress during midday in hot climates with behavioural thermoregulation, e.g., finding shadow places, building shelter (Parsons 2003, 44-46) or entering water when available (see chapter 5.4.2). As already shown in chapter 3.4.3 the avoidance of heat stress by seeking shade in humans was finally acknowledged by Wheeler in later publications (Wheeler 1993; 1994c). However, he did so without pointing to the contradiction that emerged from his divergent models. This contradiction leads to a loss of explanatory power of his earlier sun-streamlined hypothesis concerning the *emergence* of bipedalism and the loss of body hair. Similarly, it affects the aspect of the interlocking point in the emergence of these features.

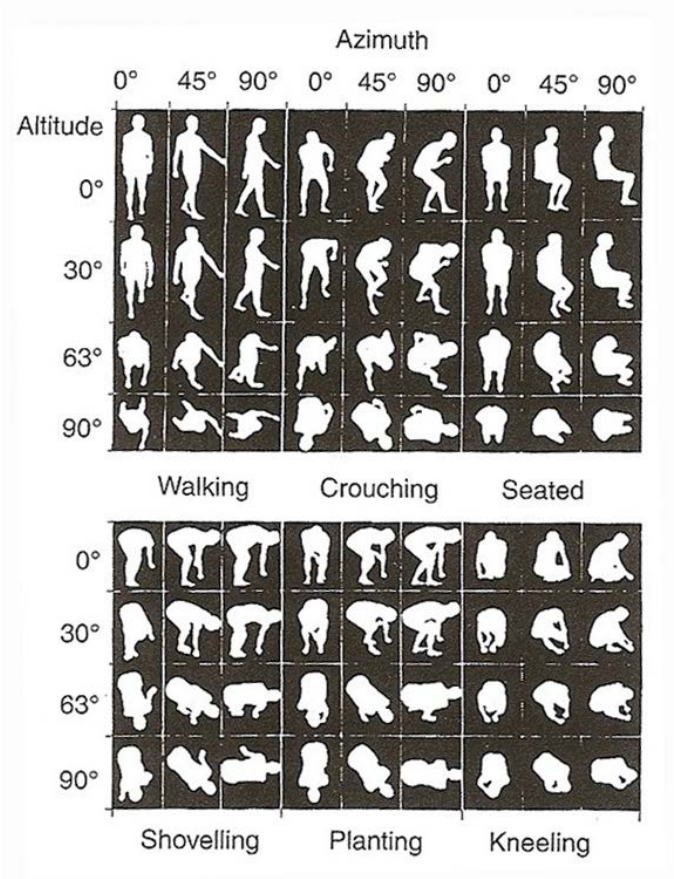


Figure 6.2 Underwood and Ward showed a selection of silhouettes of a subject in various postures, corresponding to the area illuminated by the sun's rays at different angles of altitude and azimuth. Some of these silhouettes represent realistic postures that hominins would adopt if exploring real savannah grasslands, e.g., during gathering or hunting. Adapted from Underwood and Ward (1966)

A similar degree of oversimplification concerning the environmental context of early hominin evolution is implied in several aquatic hypotheses. For example, Hardy proposed that bipedal gait developed when early hominins stood in water in an upright posture to keep the head above surface (Hardy 1960b); the same argument was repeated by several proponents of the aquatic hypotheses . However, as mentioned above and in chapter 4, upright posture is adopted by several primate species in water, even in very shallow water, sometimes even on wet ground. In several cases where primates stand upright in water (see Fig. 6.3), they are not doing so only to keep their heads out of the water and so increasing their chances of survival, as often argued. In fact, wading in primates can occur both in a bipedal as well as in quadrupedal gait (see chapter 4). In apes, wading in an upright posture is completely compatible with quadrupedal locomotion on land (see data in chapter 4.3.3). This was a major problem of Hardy's wading ideas and other versions of his wading hypotheses (Kuliukas 2011a; Niemitz 2002).

It is important to note that the argument toward an alleged increased survival benefit of an early hominin standing upright in water can also be applied to the functional focus of other organisms which interact with large bodies of water. For example, postural behaviours of several terrestrial species like bears could be interpreted as "adaptive" to a semi-aquatic environment (see Fig. 6.3). However, the expression "adaptive" is barely justifiable: bears can stand upright in water, but they probably do so more often in connection with a terrestrial environment. On the other hand, bears can show a broad range of intraspecific behaviours towards water, as shown by the the Swiss biologist David Bittner, who investigated for years wild Kodiak bears (*Ursus arctos middendorffi*) and coastal brown bears (*U. a. horribilis*) in Alaska. Some individuals seem to enter water and wade and swim in situations in which water contact would not be necessary; other bears seem to avoid entering water or wetting their ears as much as possible (pers. comm.). Please note that the term "terrestrial" to describe bears is relative, since the fact that a terrestrial organism is able to swim justifies the use of another term. However, the term "semi-aquatic" is traditionally used in connection with organisms with highly specialized aquatic traits. Bears are rather "semi-aquatic" when compared with other terrestrial mammals. Kodiak bears, for example, are able to dive when searching for food at the bottom of a rather deep part of a lake. [79]

Similarly problematic is the term "adaptation" when employed in association to great apes' interaction with water. The use of statistic methods to quantify this behaviour, to compare it with terrestrial bipedalism and to interpret it as evolutionary meaningful – as carried out by Kuliukas (2001; 2002) in observations of wading bonobos (*Pan paniscus*) – is questionable, as the most important substrate in which an orthograde postural behaviour of bonobos is not a terrestrial but a semi-arboreal habitat – they usually move quadrupedally on land (D'Aout et al. 2004; Doran & Hunt 1996; Kano 1980; 1983; Kano & Mulavwa 1984; Kortlandt 1995; Susman et al. 1980; Susman 1984b). As explained by Kano, bonobos "probably spend the highest proportion of their time in the upper tree layer" and "no other primate species uses such diverse food types and strata as the pygmy chimpanzee" (Kano 1992, 122). My criticism is not directed against the whole research carried out by Kuliukas, only against his comparison between terrestrial bipedalism and wading and his use of statistics in a dataset with categories containing very low numbers. However, his attempt to collect data on wading bonobos and test his hypothesis empirically has to be acknowledged.

[79] See https://www.youtube.com/watch?v=D_5DoQK4-0A, retrieved on 15 March 2014.



(A)



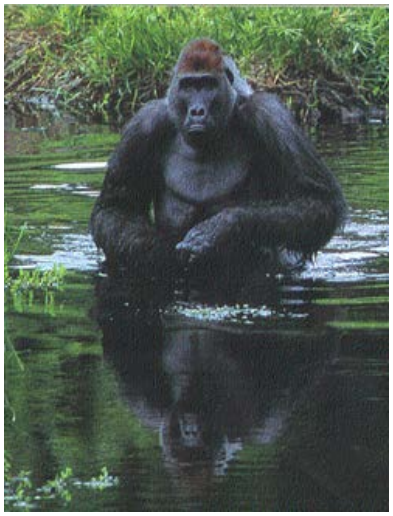
(B)



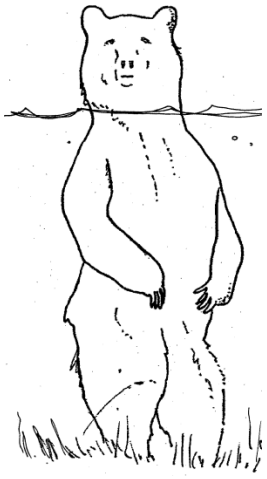
(C)



(D)



(E)



(F)

Figure 6.3 Mammals standing upright in water. (A) A wild female with her infant and (B) a captive orangutan (*Pongo*) wading upright holding a stick in a water depth that would probably allow standing quadrupedally; (C) captive common chimpanzee (*Pan troglodytes*), Cooper, standing upright in a swimming pool – quadrupedal posture is not possible at this water depth; (D) baboons (*Papio*) wading quadrupedally and bipedally in very shallow water in the Okavango Delta; (E) a wild Western lowland gorilla (*Gorilla gorilla gorilla*) wading upright in Mbeli Bai, Congo – here a quadrupedal wading is probably not possible; (F) bears (Ursidae) sometimes adopt an upright posture in water, but similar to primates revert to quadrupedal locomotion on land. (A) after photograpy in *National Geographic*, June 1980; (B) after Napier (1971b); (C) photography by Nicole Bender; (D) photography from a scene in the documentary *Planet Earth*, Part 1;[80](E) photography by Chadwick published in *National Geographic*, July 1995; (F) modified from Bender (1999).

The main question regarding Hardy's hypothesis of wading (and swimming and diving) as factors responsible for the emergence of hominin bipedal gait is: why should an early hominin adopt a bipedal posture in a terrestrial environment? As explained in point (A) above, bipedalism as a deviation of quadrupedal gait observed in other primates has to be regarded as costly trait which needs a clear justification for its *emergence* in connection with a real environment. As bipedalism can also be observed in primates wading in very shallow water, the alleged advantage of a hominin holding the head above water does not explain or justify the emergence of a habitual bipedal gait as an adaptation to a semi-aquatic environment. An upright posture in chest-deep water is also questionable to supply a selective regime for the development of a bipedal gait. The exploitation of aquatic food resources (as observed in several human populations) can be carried out without entering chest-deep water (see "strandlopers" in chapter 6.7 and chapter 4.2.5 on baboons eating shell-fish obtained from the coastal rocks in South Africa). The same difficulty can be found in several hypotheses on the emergence of hominin bipedalism in diverse environments – bouts of upright stance or bipedal gait over short distances are not rare among primates, as explained in point (A). The expression *habitual bipedalism-paradox* is suggested here to refer to the problems of a facultative bipedalism being efficient enough and more flexible than a habitual bipedalism to fulfil the functions seen as crucial for the emergence of the bipedal gait in early hominins. With very few exceptions, primates regularly move on four legs on the ground. The facultative bipedalism used in special situations both in terrestrial as well as in arboreal contexts (see above) allows a flexible postural interaction with the environment by keeping

[80] See https://www.youtube.com/watch?v=nAiZFhhHEXU, retrieved on 15 March 2014.

the quadrupedal locomotion which was selected in ancestor stages (assuming that the last common ancestor of panins/hominins was able to move quadrupedally on the ground sporadically). I suspect that the most common reasons for using oversimplified ideas to contextualize the evolution of early hominins is the need to conceal problematic aspects of one's own hypothesis – problems which are ultimately a product of the difficulties in solving the habitual bipedalism-paradox. It is often easier to change, oversimplify, or keep obscure the environment in which an organism may develop a certain trait than to clearly explain the pitfalls of the hypothesis when assuming a real environment.

6.6 Unprofitability hypothesis on early hominin evolution

A hypothesis based on the convergence approach that addresses the problems related to the interlocking point and the habitual bipedalism-paradox is proposed here. It is suggested that the initial stages of habitual bipedalism evolved as an anti-predatory strategy.

Anti-predatory strategies are well studied from several perspectives in diverse biological fields.[81] When a predator sees or has approached a prey, it has to make important decisions about the profitability of the prey (Caro 2005, 225-263, 305-333). Some preys are more profitable than others. An unprofitable organism is protected by noxious chemicals, stings or spines, is unpalatable or poisonous, or able to eliminate the element of surprise by detecting the predator from a distance in which it can easily outdistance the predator. The decision to attack a prey is also dependent on anatomical structures like horns, feet/claws and teeth that a prey can use to seriously hurt the predator. Several organisms are protected because they are much larger and stronger than the predator and more likely to cause a predator injury - elephants, rhinoceros and buffaloes often attack a predator that has infringed their critical distance (Cloudsley-Thompson 1980, 190). Different anatomical and behavioural traits allow

[81] Pioneer studies of prey-predator relations in carnivores were carried out by Kruuk and Turner (1967), Kruuk (1972), and Schaler (1972); for an overview of the role of predation in animal life see Curio (1976); for an encyclopaedic work on anti-predatory strategies in birds and mammals see Caro (2005). Several investigations treated a broad range of topics related to predation (and parasites and diseases) in different taxonomic groups (Caro & Fitzgibbon 1992; Crawley 1992a; Crawley 1992b; Crawley & Krebs 1992; Hanski 1992; Harvey & Gittleman 1992; May & Watts 1992; Newton 1992; Northridge & Beddington 1992; Riechert 1992; Sabelis 1992; Seger 1992; Underwood & Fairweather 1992). The specific topic prey defence is reviewed by Guilford (1992), Malcom (1992) and Wickler (1971b); different aspects of recognition and localization of predators and prey from the point of view of behavioural neurobiology are treated by Carew (2000). Anti-predatory mechanisms is an important issue in the investigations of functional and causal aspects of nest distribution, one aspect which was central in the investigations carried out by Tinbergen (1953; 1959); see also Veen (1977). On the role of social learning in connection with anti-predatory strategies in mammals see Box and Gibson (1999) and other chapters in the same volume.

some organisms to resist the attack of several predators or at least make the hunting costly (Cloudsley-Thompson 1980, 70): some animals are specialized in armoured defence, like pangolins (Manidae) and armadillos (Dasypodidae), or have a thickened skin, like elephants, hippopotami and rhinoceroses, or have a thick and loose epidermis that is difficult for a predator to penetrate or to grip and suffocate the animal, like the honey badger (*Mellivora capensis*) and European badger (*Meles meles*). These two species are able to "twist inside" their own skin and bite predators. Honey badgers and wolverines (*Gulo gulo*) are good examples of animals characterized by a notorious ferocity, stubbornness and tirelessness when defending themselves (Caro 2005, 417; Kruska 1988).[82] Unprofitable organisms often developed conspicuous signals to advertise unprofitability (Darwin 1871; Poulton 1890; Wallace 1870). Well known are the cases of the aposematism (warning coloration) of poison frogs (Dendrobatidae) (Summers 2003) and several insects (Beatty et al. 2004; Gilbert 1983; Grant 1963; Guilford 1992; Heikertinger 1940; Malcolm 1992; Ruxton et al. 2004; Wickler 1971b).

It is proposed here that bipedalism in early hominins did not evolve as an advantage related to locomotion, thermoregulation or as alleged postural or locomotory advantage in water or other substrate (see Tables 6.2-6.5). As discussed above in points (A) and (F), these hypotheses do not offer clear reasons for the development of *habitual* bipedalism and leave unanswered the question of the habitual bipedalism-paradox and the interlocking point aspect of an incipient habitual bipedalism. It is suggested here that bipedalism evolved as a conspicuous signal to advertise unprofitability. I came to this conclusion during the investigations for my diploma-work on human evolution in the early 1990s. I was surprised to see how many illustrations of primates in early books on natural history depicted hairless primates with a stick in the hand (Bender 1999, 16-18). These anthropomorphic depictions were interpreted as an expression of what humans perceive as their self-image (*Selbstbild*) (Bender 1999, 16). I began to think of the possibility that predators quickly associate human bipedalism as a warning signal. According to the information of a Samburu man (Ngala Lepuchirit, pers. comm.), Samburus and Maasais (semi-nomadic people of Kenya and Tanzania) believe that lions are able to recognize a man holding a spear or a stick in the hand

[82] Video footage shows that a leopard was able to kill a honey badger, but only after one hour of fight. Another footage shows a honey badger fending off six lions and eventually escaping; both videos in http://www.slate.com/blogs/quora/2013/10/24/animal_fights_can_a_honey_badger_win_a_fight_with_a_wolverine.html, retrieved on 18 March 2014.

as a warning signal. The assumption of spears functional as signals is also implied by Frump (2006, 72), who stated that the lions in the Kruger Park in South Africa lost their fear of large spear-bearing hunting parties or white men with guns as a consequence of their protected status.

Unfortunately, no studies on the effect of efficient anti-predator strategies by humans against lions exist (Löe & Röskaft 2004). According to anecdotal data, there are at least two strategies used by humans when facing[83] a lion or a group of lions: bluffing and freezing. The bluffing is described on a popular website[84]: raise the arms, shout and clap the hands. A similar strategy was reported by Alexandre Poussin, who walked from Cape Town to Cairo together with his wife Sonia. Once they suddenly encountered a group of nine to ten lions with cubs hidden in tall grass thirty meters away. Their guide Robby Bryden started running towards the lions, shouting and clapping his hands, indicating to the Poussins to do the same; the lions ran away (Alexandre Poussin, pers. comm.). Staying completely motionless when suddenly facing a lion is used by Samburu and Maasai. A Samburu told me that he encountered a lioness when he was a teenager in Kenya. He first mistook her for a large dog; after he saw that it was a lion, he stood several minutes motionless until the lioness left (Ngala Lepuchirit, per. comm.). The same strategy is described by other so-called "bush smart" people, i.e., people with experience in the African bush and its wildlife and aware of efficient anti-predatory strategies against large predators. For example, when refugees crossed Kruger National Park at night in an attempt to clandestinely enter South Africa from Mozambique, they often encountered hunting lions. Following the previous instructions of the guide, the whole group had to stay completely motionless and wait for the lions to go away. The Mozambican John Khoza described one encounter with lions in a night of July 1972 at the age of fifteen: "I stopped. I froze. We all did. I faced the lion in front of me. But I knew too there were at least two or three to the rear. Always, there are lions to the rear. We stopped. We waited. We did not move. We were absolutely still. Ten minutes passed. Fifteen minutes passed. Then we did not count the time" (Khoza in Frump 2006, 74). Frump, who interviewed Khoza, described the reaction of the lions as follows: "Eventually, seeing no obvious vulnerabilities, seeing no trigger signs, the lions moved on to easier, surer prey" (Frump 2006,

[83] When so-called "man-eater" lions approach a human undiscovered, it seems that they prefer to hunt humans behaving "abnormally", such as inebriated or injured people as well as persons on bicycles (Kerbis Peterhans & Gnoske 2001).

[84] http://www.wikihow.com/Survive-a-Lion-Attack, retrieved 31 Juliy, 2014.

74). Such encounters can occur several times per night (Frump 2006, 74). People without experience and without a guide, tend to panic and run away and are mostly killed. The expression “Whatever you do, don’t run” is common in Africa (and not only there) and summarizes what is usually considered as the most important rule when facing a dangerous predator (Allison 2007; Frump 2006; Hood et al. 2006).

Incipient habitual bipedalism in early hominins evolved according to my hypothesis when two conditions were met:

1. The semi-arboreal ancestor of first hominins was exposed to high predatory pressure when moving on a terrestrial substrate during the day[85].

2. Single individuals of this species were able to defend themselves successfully against predators by staying motionless and/or using a primitive tool – possibly a long stick.

If these two conditions were met, habitual bipedalism could evolve as a signal for unprofitability (see below). The combination upright posture and use of a stick for defence would represent an immediate selective advantage and favour the dissemination of this behavioural trait in the population. The unprofitability hypothesis does not imply a higher level of skill in manipulating tools than observed in wild common chimpanzees. For observations on the use of tools in wild common chimpanzees see Pruetz and Bertolani (2007), Nishida and Hiraiwa (1982); Boesch and Boesch (1981); McBeath and McGrew (1982); see also several references on tool-use in aquatic activities in chapter 4.3.3.

Some authors proposed (sometimes only briefly) that bipedalism might have been used as part of threat displays to defend against predators or as an intraspecific appeasing signal or for sexual display; see, e.g., Clark (1960), Livingstone (1962), Wescott (1967a, 738; 1967b); Guthrie (1970); Jablonski and Chaplin (1993) and Jordania (2011). Kortlandt (1980) suggested that early hominins might have used thorn branches in order to defend themselves against their natural enemies in an open environment. In opposition to the here proposed hypothesis, most of these ideas were formulated within the context of the savannah hypotheses, did not mention comparative data and did not supply data on the use of sticks in apes in connection with bipedalism in water. It is not assumed here that sexual display was the

[85] It is assumed here that early hominins were using trees (as all extant great apes) or rocky cliffs (as geladas, *Theropithecus gelada*) for sleeping at night. See chapter 6.3.2 for evidence on arboreal adaptations in early hominins.

only factor in the emergence of incipient bipedalism, although the aspect of sexual selection has to be considered in connection with the dissemination of permanent bipedalism.

One possible difficulty of the here proposed hypothesis is related to the idea that the use of a stick demands a degree of cognitive ability and purposefulness that is not expected in very early hominins in the light of available evidence. Although we know now on the use of wooden spears to kill and extract bush babies from cavities of hollow branches or tree trunks by common chimpanzees in Fongoli, Senegal (Pruetz & Bertolani 2007), the use of sticks is not part of the regular behavioural repertoire of most extant apes. However, the unprofitability hypothesis does not imply purposefulness or high levels of cognition in early hominins. Although extant apes actually do not use sticks in environments or situations usually regarded as relevant for the contextualization of early hominins, my review of primates' interaction with water reveals that sticks are used in a context that is not considered in mainstream palaeoanthropological literature: when entering water. Sticks were used by wild, semi-free ranging and captive apes for the purpose of testing water depth and for support during wading (see chapter 4.3.3). The unprofitability hypothesis does not necessarily assume as a pre-condition that incipient habitual bipedalism emerged in association with wading, as there are other possible scenarios in which sticks might be used. However, according to my data, water is the only context in which bipedalism in association with the use of a stick occurs regularly; I prefer to formulate the hypothesis based on the available evidence. To accommodate the possibility that further findings demonstrate that bipedalism and the use of a stick were observed (together) in other contexts, it is preferred here to keep the environmental aspect more general, as it will not affect the determining argument (that habitual bipedalism developed as a signal to advertise predators).

It is important to note that the argumentation of incipient habitual bipedalism emerging in connection with wading does not imply that this was the only or the most important habitat of early hominins. Proponents of the aquatic hypothesis assumed that the search for food in a semi-aquatic environment was the crucial aspect in the emergence of bipedalism (1960a; Hardy 1960b; Morgan 1972). In the here proposed hypothesis, however, the pivotal aspect is not the exploitation of food resources in a semi-aquatic environment, but the occasional wading to cross water barriers and a *possible* (but not dogmatic and not absolutely necessary) exploitation of aquatic food resources; these two possibilities are not mutually exclusive and both do not require any specific adaptation to water use in early hominins, as suggested in the

aquatic hypotheses. The unprofitability hypothesis is conceivable in different shallow-water habitats such as river-floodplains, patchy wetland forests or estuaries; see Wrangham (2005; 2009) for a hypothesis acknowledging such landscapes in connection with early hominin evolution. To date, we do not have conclusive data on where and when exactly the initial stages of early hominin habitual bipedalism emerged. Therefore, the unprofitability hypothesis refers to the theoretical aspect of an early hominin unable to swim and regularly wading in an upright posture. As in extant apes, the specific environment is not relevant for the bipedal wading – as shown in chapter 4.3.3, apes were observed wading bipedally in several environmental contexts. As already noted, in a more general view, the unprofitability hypothesis also conceives other environments where the association between bipedalism and anti-predatory strategy could theoretically emerge. Therefore, the verification of the hypothesis and the prediction of new findings do not depend on a specific environment, but from the here proposed link between postural behaviour and anti-predatory strategy. This link can be verified by comparative data on patterns of unprofitability in a wide range of taxa and by possible experimental approaches testing the assumption of human bipedalism/stick use as an efficient signal to warn predators.

The use of sticks for defence associated with an upright gait would represent a major shift in the functional focus of early hominins. One of the consequences of this anti-predatory strategy is the possibility of exploring a wider range of environments – actually any environment in which the anti-predatory strategy could be efficiently employed. The exploitation of several environments beside the habitual semi-arboreal habitats would lead to a relaxed selective pressure on several key hominin features that were optimized in a semi-arboreal habitat. For example, as shown in chapter 6.8.1, humans have a larger amount of subcutaneous fat than other primates and most other terrestrial mammals. Unfortunately, data on fat tissue in early hominins is not available to date. Recently, the reconstruction of body mass in several extinct hominins was published by Gallagher (2013), without reference to body fat. The lack of data on fat tissue in extinct hominins and scarce data on fat tissue in primates has to be addressed in further investigations. It is conceivable that new approaches for genetic data analyses and advances in genetic investigation technology will supply at least some hints on a possible association between the emergence of bipedalism, the increasing reduction of body hair and the initial stages of the increasing amount of fat tissue in early hominins. However, such investigations are very complex, as a large amount of body fat in

modern humans is not associated with single genes, but to a large number of genes (Xia & Grant 2013); the same probably applies to early hominins. In fact, in-depth analyses of the association of single genes and obesity markers often do not yield positive results (Bender *et al.* 2011). Although to date it is not possible to give any conclusive answer on when and under which selective pressure this trait evolved, it is reasonable to assume that an unprofitable ape would afford to have a large amount of body fat – and therefore probably be slower – than a semi-arboreal ape. This specific argument is compatible with comparative data on unprofitable preys, which often exhibit slower and more predicable movement than unprotected species (Sherratt et al. 2004). It is sometimes assumed that the essential aspect of the difference between humans and other primates in the amount of fat tissue is that "the evolutionary transition to the large-brained hominids from arboreal anthropoid ancestors hinged on abandoning the fat-limiting arboreal niche and adopting new 'fat-friendly' terrestrial habitats" (Dittus 2013, 9).

Although I agree with Dittus' argument on the arboreal niche as a fat-limiting factor, he points out to the fact that humans have usually more body fat than other terrestrial mammals, including terrestrial primates (see references in chapter 6.8.1). This indicates that the terrestriality alone does not explain this specific difference in body composition. It is suggested here that the main factor responsible for the large amount of fat tissue in humans is the habitual bipedalism/the use of sticks evolved as a signal for unprofitability and as an active anti-predatory strategy. This strategy had the effect that hominins could afford to be slow – an agile locomotion was not needed, since early hominins were in this stage of evolution probably not specialised cursorial hunters. According to my hypothesis, with the adoption of a habitual bipedalism the most important behavioural trait to be optimized was a dogged and organized defence against predators.

As already stated above, in opposition to the aquatic hypotheses, the unprofitability hypothesis does not necessarily assume that regular exploitation of aquatic food resources was the initial factor in the development of habitual bipedalism. However, as soon as first hominins relaxed their strong dependency on forests, such an interaction with a semi-aquatic environment would be feasible. Bipedalism in such an interaction would be irrelevant from the point of view of locomotion or postural behaviour. In fact, some apes are able to learn to swim, dive and wade without the anatomy of habitual bipeds (see chapter 4.4). Several primates and most terrestrial mammals are able to swim using a dog-paddle. An early hominin

using habitual bipedalism to keep his head above the water surface is not essentially different from a quadrupedal ape using a facultative upright posture in the same environment. By adopting the unprofitability hypothesis, several hypotheses proposed to explain the emergence of bipedalism would have an explanation of the interlocking point of the initial bipedalism, and could be used to explain several aspects of an optimization of a habitual bipedalism in connection with various situations, as carrying or vigilance. In such cases, bipedalism could not be called “an adaptation for vigilance” (or carrying, etc.), but as part of the functional focus of an early hominin walking on two legs (the bipedalism evolved in association with other factors).

How can the unprofitability hypothesis be tested through fossil evidence? It cannot, at least not to date. Wooded tools are usually not fossilized, and the exact events in which the habitual bipedalism emerged can barely be reconstructed. I would like to present the unprofitability hypothesis as a model to illustrate how hypotheses which cannot be corroborated by fossil evidence have a justification when they are based on comparative data and theoretical considerations. It is suggested here that the evaluation of these hypotheses can be carried out by evaluating the comparative data and the arguments outlined in the theoretical framework of the proposed model.

This leads to an important question. It is proposed here that hypotheses based on fossil evidence are stronger when they focus on traits which are “optimized enough” to be clearly recognized in the fossil evidence. However, the anatomy of early hominins in the stages when incipient habitual bipedalism emerged probably cannot be distinguished from the anatomy of the ancestor of first hominins which were only facultatively bipedal. This statement is central to understanding why the evaluation of the hominin status of *Ardipithecus* is so controversially discussed. Incipient traits are often intrinsically linked to behavioural traits and these are mostly not visible in fossils. However, through the use of the convergence approach presented in this thesis, we can create a theoretical framework to discuss how such incipient traits might have developed convergently in different taxa; the fossil evidence can be used to verify predictions on stages in the evolution of a trait which can be recognized in the fossil evidence.

6.7 Summary of the evaluation of hypotheses

Arguments used in several models of early hominin evolution are often based on oversimplified generalizations concerning the environment of early hominins and adaptive traits evolved in response to these environments. Common problems that have emerged in the comparisons of savannah and aquatic hypotheses are strategies used to accommodate discrepancies: (a) being obscure about the adaptive meaning of traits (or not mentioning these traits at all) that do not fit the specific hypothesis, (b) conceiving oversimplified environments, (c) producing auxiliary hypotheses characterized by a high degree of biological implausibility and (d) comparing hominins with distantly related organisms using biological constellations. Another typical problem in scenarios on early hominin evolution is the tendency to associate key evolutionary events with climatic changes, often with a wide range of temporal and geographical placement of the considered events. In opposition to these models, hypotheses usually treated as non-controversial are often based on sound comparisons between distantly related species, using clear patterns of functionality and avoiding scenarios with a degree of resolution that cannot be corroborated with available evidence or unambiguous theoretical considerations; see several examples in (Conway Morris 2008; Koepcke 1971; 1973; McGhee 2011) in several other references in chapter 3 and Appendix C In cases in which extant analogous organisms to the studied species are missing – e.g., in the discussion on the functionality of long saber-shaped canine teeth in saber tooth cats (see chapter 2.4) – the debate on the adaptive value of traits is characterized by multiple hypotheses.

In different parts of the present thesis, several arguments of the aquatic hypotheses were criticized. However, it is important to differentiate between the dogmatic pro and con discussion of the aquatic models and on gathering and discussing data related to water use in primates, in an attempt to make verifiable predictions on new research findings on hominoid and early hominin evolution. It is often assumed that the aquatic hypotheses are not scientific. This view is rejected here. It is certainly true that several arguments of the aquatic hypotheses are flawed – some of these arguments are probably perceived as the most flawed concepts published after the modern synthesis. However, it is important to consider the different ways in which specialists perceive the aquatic model. Some students of human evolution immediately recognized the flawed aspects of several aquatic model arguments as the uncritical comparison with highly specialized aquatic organisms or the feminist discourse

used in Elaine Morgan's first book on the aquatic model (Morgan 1972). Instead they ignored these aspects and focused on the challenging aspects of early hominins exploiting aquatic food resources – a completely different scenario than the classic savannah hypotheses. The majority of palaeoanthropologists has regarded the aquatic hypotheses as a disturbing component in the debate on human evolution and stressed only the obvious negative aspects of this idea. This is still the prevalent attitude today. However, a comparison between aquatic and some early hominin evolution classic ideas illustrates (see chapter 3.4.2) that the differences between the two models are less pronounced than most palaeoanthropologists might assume. Concerning the use of convergences as a tool in adaptive analyses, both theoretical models show serious methodological problems. In the aquatic hypotheses, the methodological problems are related to two different phenomena. On one hand, several arguments refer to early hominins exploring a coastal environment and developing physiological and anatomical adaptations associated to swimming and diving, often compared with adaptive traits found in highly aquatic organisms; classic examples are the large brain, naked skin and ventro-ventral copulation of dolphins and humans (Langdon 1997).

On the other hand, it is surprising that both proponents as well as critics of the aquatic hypotheses do not point out the elementary detail that the exploitation of marine food resources by primates (including humans) does not require diving. For example, in South African rocky shorelines with a substantial exposure of a great variety of shellfish available at low tides, the gathering of shellfish does not require even wading (own observation).[86] Early colonial settlers at the Cape in South Africa noted that the San-derived people frequented the shorelines in search of marine animals. They referred to these people as strandlopers or "beachcombers" (Parkington 2006). I regard such an exploitation of aquatic food resources as a conceivable model to contextualize early hominin evolution, although this idea will not be developed here.

[86] For reviews on primates exploiting aquatic food resources see chapter 4.2.5 and 4.3.3; human exploitation of marine and freshwater resources in different parts of the world was treated by several authors (Bailey et al. 2007; Bailey et al. 2008; Bailey 2009; Bailey & Milner 2002; Bailey & Parkington 1988 and other chapters of the same volume; Broadhurst et al. 2011; Brothwell & Dimbleby 1981 and other chapters of the same volume; Erlandson & Rick 2008 and other chapters of the same volume; Fischer & Myrhøj 1995 and other chapters of the same volume; Joordens 2011; Klein et al. 2004; Koyama & Thomas 1981 and other chapters of the same volume; Meehan 1977a; Meehan 1977b; Meehan & White 1990 and other chapters of the same volume; Nishimura 1973; Noll 2002; Parkington et al. 1988; Parkington 2006; Shackleton 1988; Sopher 1965; Stewart & Cunnane 2010 and other chapters of the same volume; Waselkov 1987); see also references in Table 6.4.

To summarise, there are three main attitudes concerning water use in primates within palaeoanthropological research. (a) Discussion on potential water use in early hominins is considered as unneeded or only justified in concise attempts to discredit or falsify aquatic hypotheses. This is the most common attitude among palaeoanthropologists who have expressed their opinion on this topic (see Table 6.4 for references). The strong connection between the topic "water use in primates" with the general picture of hominins depicted as "living like dolphins or penguins"[87] is probably responsible for the popularity of this attitude. (b) Some authors have suggested merging classical ideas on hominins evolving on grassland savannah or mosaic habitats with the aquatic hypotheses. This view uses the picture of "early hominins as living like dolphins and penguins" to justify the need of a "savannah/aquatic" hypothesis in which early hominins were not fully aquatic, but only able to explore shallow water by swimming, diving and wading (see Table 6.4 for references). Factually, this merged version is indistinguishable from the ideas proposed by Alister Hardy and Elaine Morgan. (c) The approach defended here is based on the following argument: in terrestrial animals, data on water use is essential, even for species known not to be able to swim (as apes); the justification for this statement is that for non-swimming terrestrial organisms water bodies represent efficient barriers to their dispersal (see chapter 4.3.6). The discussion on water use does not necessarily imply that the studied organisms must have had specific adaptive traits selected in connection with an aquatic environment. I propose discussing the role of water in early hominin evolution objectively, avoiding the temptation to formulate hypotheses "explaining" a large number of traits in a single scenario without proper data and without considering the possibility that some traits evolved in response to different selective regimes. Similarly important is to avoid the pitfalls of dogmatic debates in the sense of "savannah versus aquatic hypotheses".

[87] See chapter 3.4.2 where I explain that the picture of hominins "living like dolphins" is more often propagated by critics of the aquatic hypotheses than by the champions of the idea. Another influential component in the negative reception of the aquatic hypotheses is related to the widespread opinion among palaeoanthropologists in the 1970s and 1980s that the savannah model was a fact, not a theoretical concept (see Appendix D). Another aspect rarely mentioned in the literature is that in several other species "aquatic hypotheses" are discussed, without the emotional involvement observed in palaeoanthropology. For example, in several publications in the 19th and early 20th century, sauropod dinosaurs were often depicted as exploring an aquatic environment (Henderson 2004); see Thewissen and Taylor (2007) for a review on modern hypotheses on aquatic adaptations in the limbs of basal amniotes. The emotional component of the "aquatic ape" discussion is probably related to the fact that we are investigating the evolution of our own species.

6.8 Application of the convergence approach on swimming and diving ability in hominoids

6.8.1 Discussion of Angus' low fat hypothesis on swimming

In an influential paper, Shannon Angus (1971) stated that chimpanzees' apparent inability to swim is primarily a consequence of a low ratio of fat to muscle in this species. Angus' main arguments were based on two facts. First, she assumed a value of 9% as the average body fat by weight in chimpanzees, which was estimated by other investigators (Hodson et al. 1967) through an indirect method. Second, she started from the premise that humans have an average of 20% of body fat by weight (Hodson, pers. comm. in Angus 1971). She hypothesized that "this difference of 11% may be the crucial factor in explaining why humans can learn to swim and chimpanzees cannot" (Angus 1971, 52). Additionally, she reinforced her hypothesis through the assumption that "obese humans find it easy to float on water, while persons with extremely heavy muscle development report that they are unable to float, and they find that learning to swim is difficult" (Angus 1971, 52), not giving references for this statement.

Several aspects of Angus' hypothesis shall be discussed here, both concerning the data she uses as also her inferences from this data. First, Angus' hypothesis does not compare chimpanzees' body fat percentage with that of other primates. Dissected adipose tissue from wild toque macaques (*Macaca sinica*) accounted for 2.1 % of body weight (Dittus 2013). In a sample of 31 sedentary, ad libitum-fed monkeys (29 crab-eating macaques, *Macaca fascicularis* and 2 pig-tailed macaques, *Macaca nemestrina*), it was found that most specimens had less than 5% by weight of adipose tissue; only a minority became obese on this regime (Pond & Mattacks 1987). This value is even lower than the figure of 9% body fat in chimpanzees used by Angus. This comparatively low amount of body fat and the consequent effect on buoyancy is not a detriment for swimming in most primates and other terrestrial animals. Most non-hominoid primates (see chapter 4.2), a few ape individuals (see chapter 4.4) and very slim humans are able to swim at the water surface because they use their limbs to create propulsive forces, which increase buoyancy.

Interestingly, although Angus published her paper four decades ago, it is still difficult to evaluate the data that she used on body composition in chimpanzees, since very few data on body composition in wild and captive primates are available (Dufour & Sauther 2002; Pond

1998; Videan et al. 2007; Wells 2010). Angus did not differentiate between body composition of captive and wild animals. However, it seems that the value of 9% by weight of fat is probably too high to be considered as an average for wild chimpanzees. A dissection of a female bonobo (*Pan paniscus*) and a female common chimpanzee (*Pan troglodytes*), both captive adults in good health at the time of death, showed that the bonobo had 3%, the common chimpanzee 10 % body fat (Zihlman 1984).

The problems of estimating average values for body composition in apes are not limited to captive animals. For instance, seasonal fluctuations in food availability lead to seasonal body weight fluctuation in wild chimpanzees (Basabose 2002; Tutin & Fernandez 1993; Wrangham 1977). Uehara and Nishida (1987) detected fluctuation in body weight in wild common chimpanzees, but only in adult females, not in adult males. Based on unpublished data from chimpanzees at Kanyawara (Wrangham) and chimpanzees at Mahale (Huffman), Knott (2005) concludes that there is an indirect indication that in common chimpanzees the fluctuation in adiposity is modest. The best indirect evidence to date for fat storages varying considerably in response to fluctuating food availability was demonstrated in wild orangutans (Knott 1998; Knott 2005).

As Angus (1971) referred to drowning in captive chimpanzees to corroborate her low fat hypothesis, it is important to note that captive primates seem to accumulate weight above the levels observed in wild counterparts. For instance, body tissue composition was determined through dissection of four adult captive lowland gorillas (Zihlman & McFarland 2000).The body fat percentage of one male was estimated at 19.4%; this individual had a constant body weight for 14 years. A further male was estimated at 26.6% body fat, while the value for one female was 24%. One large and obese female was estimated at 44% body fat. Similarly, orangutans, chimpanzees and bonobos are prone to obesity under certain captive conditions – as exemplified by the captive bonobo Kanzi (see pictures in Savage-Rumbaugh & Lewin 1994). These data are not compatible with Angus' argument of apes unable to swim due to their low adiposity respectively low buoyancy. In fact, drowning in apes occurred almost exclusively in captive animals, which in some cases have as much (in some cases clearly more) body fat than healthy humans.

The general value of 20% by weight of adipose tissue for human beings given by Angus is imprecise, as it does not consider the differences between males and females concerning body

composition. For instance, in an investigation among the Baka hunter-gatherers in village camps in Cameroon it was estimated that females have in average 24.3 % and males 13.6 % by weight of fat (Yamuchi et al. 2000); these results are similar to the average of healthy humans in several populations in non-western and western countries (Wells 2006; Wells 2010). The divergence in body composition between human males and females is relevant, since, according to Angus' arguments, males with less buoyancy should have more difficulty to learn to swim than females. However, to our knowledge there is no evidence that the ability to learn to swim varies according to sex. Contrary to what seems to be a popular wisdom, the ability to float at the water surface is not a relevant pre-condition to learn to swim. For instance, a considerable number of infant and adult humans are unable to float horizontally in water, as the legs will often sink (Whiting & Stembridge 1965). Through an early and intensive contact with water, very lean and obese humans are usually able to compensate these deviations of a 'normal anatomy' through adjustments in their swimming techniques. Difficulty to learn to swim is often related to psychological, not anatomical factors (Gabler 1982). Humans have usually difficulty to learn to swim when they had an insufficient habituation to shallow and deep water, after a traumatic experience in water, or after a long unpleasant experience with water (Gabler 1982; Greuter 1995; Knöpfel 1982; Whiting 1970). The fear of water can reach pathological dimensions, an anxiety disorder called aquaphobia (Líndal & Stefánsson 1993).

To sum up, Angus' low fat hypothesis is improbable on a theoretical level. The main problems with this hypothesis are that she did not consider the role of fat in the swimming ability of non-hominoid primates (which are often able to swim despite the low amount of body fat), and that her statement on the difficulty of lean humans to learn to swim is not based on empirical evidence and not supported by experience reported in literature on human swimming.

6.8.2 Saci LCA: New hypothesis on the loss on instinctive swimming in hominoids

Bender and Bender (2013) proposed a new model to explain the loss of swimming ability in hominoids, the "Saci last common ancestor (Saci LCA) hypothesis". (In Brazilian folklore Saci-Pererê is a one-legged slave child unable to cross even small streams.) This Saci LCA states that an explanation of the loss of instinctive swimming in apes should not be based on one anatomical feature of a single ape species, because the loss of swimming ability is a common feature of the whole hominoid group. We therefore suggested that the loss of

swimming ability in hominoids is best explained as a consequence of phylogenetic constraints linked to the adaptation to an arboreal life in the last common ancestor of this taxon (Fig. 6.4). A phylogenetic constraint is defined as “any result or component of the phylogenetic history of a lineage that prevents an anticipated course of evolution in that lineage” (McKitrick 1993, 307); see also (Price 2003). The Saci LCA hypothesis is based on the following arguments:

(a) The fact that most mammals are able to swim instinctively (see chapter 4.2.6) indicates that this trait may have been maintained through selective pressure. It is therefore parsimonious to assume that the lack of innate swimming is a rare trait in terrestrial vertebrates and synapomorphic in hominoids.

(b) As shown above, it is commonly agreed that extant hominoids and early hominins retained many anatomical features related to a specialized arboreal adaptation developed at an early stage in the hominoid phylogeny. Although it is still discussed how locomotor behaviour evolved in early hominoids, most specialists agree that the last common ancestor of extant hominoids was adapted to an arboreal life, showing climbing and suspensory behaviour (Pilbeam 1999; Senut 2012); reviewed in (Fleagle 1999). Bender and Bender (2013) suggested that this strong functional focus on arboreal life initiated a process characterized by decreased opportunities to interact with water bodies and consequently reduction of selective pressure to maintain innate swimming behaviour. As the doggy paddle is associated with quadrupedal walking, a deviation from terrestrial locomotion might have interfered with the fixed rhythmic action patterns responsible for innate swimming. Bender and Bender (2013) assumed that this process led to more flexible mechanisms of non-repetitive neuronal networks (Parker 2006) governing locomotion in water.

(c) Although the Saci LCA hypothesis states that the ancestor of all extant hominoids lost the ability to swim instinctively during a phase of high arboreality, it does not specify the exact causes of this loss of instinctive swimming, since it is probable that several factors were involved and it is difficult to reconstruct the exact causal pathway of this event. Bender and Bender (2013) hypothesized that a primate will increasingly avoid deep-water bodies when the risks of being exposed to water are clearly higher compared to the advantages of crossing the water bodies. Due to a mutual enhancement effect, a decreasing interaction with water bodies intensified the

disintegration of the doggy paddle. A common ancestor of all extant hominoids with a decreased ability to activate the doggy paddle would tend to minimize contact with water bodies and to develop secondary strategies to come out of the water after falling accidentally into it (for instance by grasping branches overhead). Similarly, this process led apes to increasingly use nonswimming strategies to cross streams (e.g., by leaping over small streams, using exposed stones or fallen log bridges, travelling through the canopy or wading bipedally through shallow streams).

(d) Although videotape[88] of swimming apes is available only for two individuals (videos 5 and 6), these data show how anatomical and neuromotor patterns related to an arboreal life influence their swimming movements. In orangutans, extreme mobility of the hindlimbs is frequently observed during positional behaviour in the trees (Thorpe & Crompton 2010). Functional anatomy of orangutans evolved in connection with climbing, bridging, and travelling over flexible branches in the canopy (Zihlman et al. 2011). The lateral movements of the forelimbs in Cooper and Suryia are probably the consequence of the high degree of shoulder mobility in these species, which in turn is a consequence of the brachiation, vertical climbing or suspensory positional behaviour in a common ancestor of all hominoids. This mobility allows limbs' movements in every direction, while in nonhominoid primates the anatomy of these joints is adapted for sagittal movements (Schultz 1969, 69).

[88] All videos mentioned in this chapter are displayed here: http://onlinelibrary.wiley.com/doi/10.1002/ajpa.22338/suppinfo, retrieved on 19 March 2014.

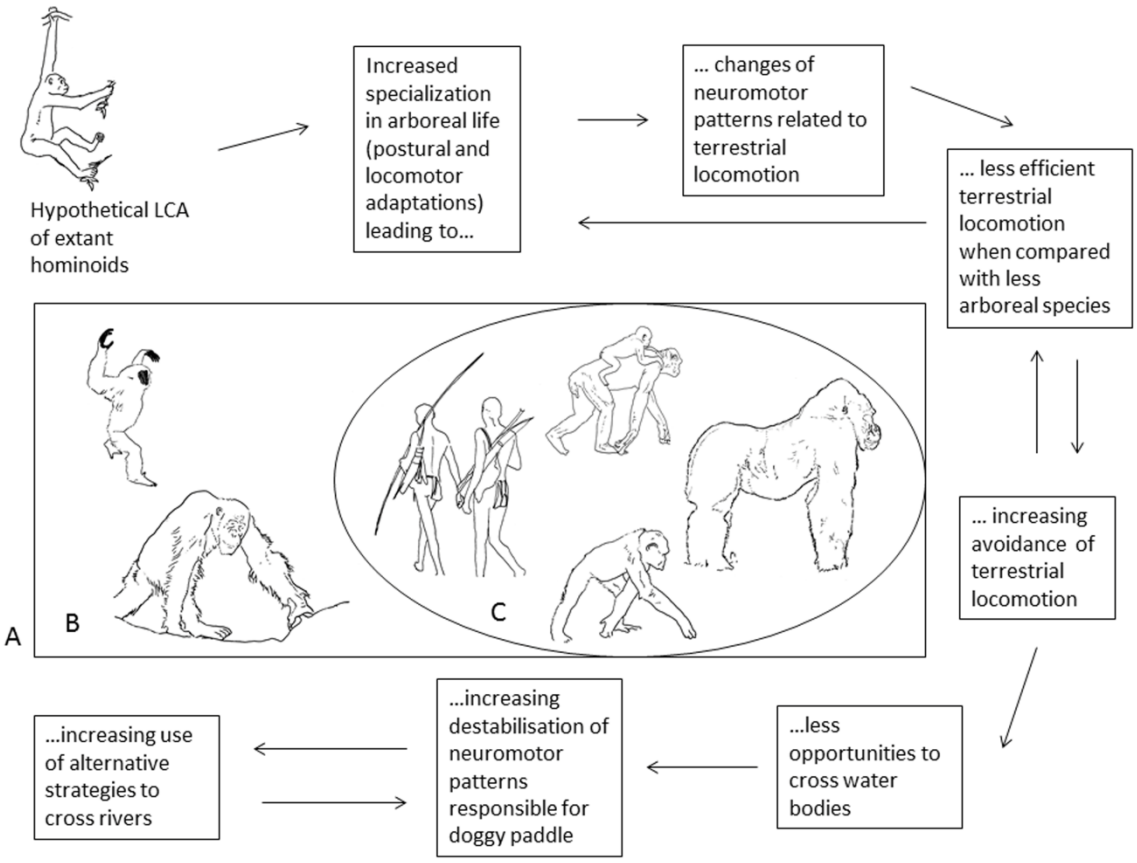


Figure 6.4 Schematic representation of the Saci LCA hypothesis. The diagram illustrates feedback loops reinforcing different elements responsible for the loss of innate swimming ability in hominoids (see text for details). (a): The high arboreality in the phylogeny of hominoids is reflected in their variable patterns of terrestrial locomotion. (b): Locomotory behaviour and anatomy in Asian apes reflect their strong focus on arboreal life. (c): Anatomy and locomotor behaviour in African hominoids reflect the secondary functional focus on terrestrial environments (figures not to scale; from (Bender & Bender 2013).

The anatomical and neuromotor changes described above are intensified through biomechanical constraints due to the deviation of limb proportions in highly arboreal primates, as for instance the development of long forelimbs in connection with brachiation. For instance, as observed in the brachiators gibbons (*Hylobates)* and semi-brachiators spider monkeys (*Ateles spp.)*, brachiation implies, among other factors, an increased ability to cross rivers through the canopy and a proportional reduction of terrestrial locomotion (Tuttle 1972; van Roosmalen 1988). In the wild, gibbons (Carpenter 1941) and spider monkeys (Campbell *et al.* 2005; van Roosmalen 1988) rarely come to the ground. Anatomical adaptations related to brachiation (e.g., shoulder joint modifications and elongated forelimbs) make terrestrial quadrupedalism more difficult both in gibbons and spider monkeys (Campbell et al. 2005;

Tuttle 1972). If they move terrestrially (what is frequently observed in captivity), they often do so on two legs (Campbell et al. 2005; Candler 1903, 187; Carpenter 1941); see also (Begun 2003).

Gibbons and spider monkeys are reluctant to enter water, and in zoos species of both groups can be kept on islands surrounded by deep water. Brachiation is more specialized in gibbons than in spider monkeys (Erikson 1963), and this difference can partially account for the divergence in swimming ability in both groups. To my knowledge, the sporadic reports of swimming behaviour in gibbons are not reliable, so that to date these species have to be viewed as unable to swim or to learn to swim. However, spider monkeys are able to swim, even if this behaviour is rarely observed (Chaves & Stoner 2010). Another species which seems to be unable to swim is the Mysore slender loris (*Loris lydekkerianus lydekkerianus*), a small nocturnal pro-simian primate endemic to Sri Lanka and South Asia. According to Shortridge, individuals of this species "when placed in water would strike out alternately with each leg in a helpless way without making any headway" (in Ryley 1913, 286). This species is also highly arboreal, spending virtually all of its time in trees, only sporadically coming to the ground (Nekaris 2001). Due to the lack of further data, however, it is difficult to state which features have a predominant negative influence on the swimming ability of this species.

The Saci LCA hypothesis does not state that all arboreal mammals have a tendency to avoid water. For example, although sloths have fore-limbs that at the first sight suggest an incompatibility with swimming behaviours, they swim both well and regularly (Anderson & Handley Jr. 2001). It is probable that due to ecological and behavioural factors, selective pressure to keep the ability to swim instinctively was constant in the phylogeny of sloths. In fact, sloths are forced to come down from the tree and walk or swim to the next tree when confronted with even small gaps in the canopy. Although highly arboreal, wild sloths come regularly to the ground to defecate and urinate (Gilmore et al. 2001).

For an evaluation of the Saci LCA hypothesis, we predict that similar phylogenetic constraints influenced terrestrial locomotor patterns and swimming ability in some other arboreal species. The prediction is not restricted to mammals. Chameleons (Chamaeleonidae), for example, lack the extensive lateral undulation typical of reptiles during gait on solid substrate. Furthermore, they developed other traits as an adaptive reponse to an arboreal life, like the zygodactylous feet, their derived body form (laterally flatened), the prehensil tail and specific

neuromotor patterns (derived gait, slow movements). Chameleons compensate the loss of undulatory movements by different adaptations, among others by high mobility in the shoulder girdle (Fischer et al. 2010).

There is contradictory data on the swimming ability of chameleons. Although some early accounts reported the lack of swimming ability in this group (see, e.g., Davenport Northrop 1891), there is anecdotal evidence on swimming in chameleons (Fynn 2011; Necas 2004). Christopher Anderson, a specialist in chameleons, states: “While they are generally regarded as having a poor swimming ability, there are known cases of species swimming actively. It is an unusual behavior and not many species are known to do it, but a couple do...“ (Anderson, pers. comm.). One chameleon (probably *Chamaeleo quilensis*) was filmed in 2011 swimming in a river in the Magaliesburg mountain range, South Africa (Fynn 2011). The chameleon was probably inflated, as it was extremely buoyant. It moved its legs in a diagonal pattern, with the legs coming out of the water during the forward movement. Sometimes it lost its balance and fell shortly on its side.

This anecdotal and contradictory data on swimming ability in chameleons can be used for the formulation of the following predictions: (1) some species are not able to swim. Some species are only able to swim if they (2a) developed secondarily the lateral undulation to propel them in water, or if they (2b) developed alternative modes of propulsive movements, or if they (2c) are able to temporarily increase buoyancy during swimming (for instance, due to the inflation of air sacs). Finally, it is possible that (3) some individuals of species which are usually able to swim are temporarily unable to swim in specific situations, for instance due to an asymmetrical inflation of air sacs, which might negatively affect lateral rotation control, causing a loss of balance around the transverse axis. In any case, a poor swimming ability or complete disintegration of instinctive swimming behaviour can only be expected in species in which the selective pressure to cross water bodies was relaxed during a considerable period of time in their phylogenies.

A further possible factor responsible for an incipient reluctance to enter water and poor swimming ability can be related to anatomical features which are not part of the locomotor apparatus. For instance, terrestrial species which were constantly exposed to water bodies in their evolutionary history developed a fur with specific features. On the one hand it fulfills the demands of the usual conditions of a terrestrial life; on the other hand it prevents the animal

from becoming completely water-soaked during swimming (Best & Hart 1976; Dagg & Windsor 1972). To determine if the fur itself or the air trapped in the fur increases flotation, detergent was rubbed in the fur of mice, rats, and gerbils; after which all of these animals swam in an almost vertical position and struggled to keep their noses above water (Dagg & Windsor 1972). Similarly, the time in which the fur was completely soaked and the total swimming time decreased significantly in Mediterranean pine voles (*Microtus duodecimcostatus*) when a wetting agent was added to the water (Giannoni et al. 1994). Because birds have hair trapped between the single follicles of their feathers, these organisms have high buoyancy in water, making swimming at the water surface easier and diving difficult. However, in some non-flying birds the feathers can get soaked with water, affecting negatively the insulation and therefore thermoregulation and buoyancy and probably the swimming ability. For instance, penguins, although highly adapted to a semiaquatic life, are prone to drown in early age, since young birds may suffer greater heat loss and loss of buoyancy in water when the plumage is incomplete (Müller-Schwarze & Müller-Schwarze 1975, 76). Opposed to this, the newly hatched hoatzin (*Opisthocomus hoazin*), a tropical bird with no recognizable adaptation to a semiaquatic life, shows a specific aquatic ability at an early age: when detected by a predator, the fledgling drops into the water and swims under the surface back to the shore (Morgan 1896, 66).

Since experiments with primates in water are unacceptable for ethical reasons, it is difficult to evaluate the role of fur in the swimming ability of primates. Given the fact that some arboreal primates rarely go to the ground and therefore have a small probability to encounter a watercourse during terrestrial locomotion, it is conceivable that some of these species developed a fur that is highly adapted for an arboreal life, but poorly suited for swimming. For instance, the fur of the highly arboreal monkeys of the genus *Callicebus* is described as long and soft (Geissmann 2003, 158). Several individuals of these species quickly drowned after falling accidentally into the water (van Roosmalen *et al.* 2002). However, as reported in chapter 4.2.4, there are reports on *Callithrix* swimming, despite soaking of the fur (Hershkowitz 1977, 560). Currently, it is not possible to be conclusive on the role of the fur in the swimming ability of species belonging to the genera *Callicebus* and *Callithrix*.

An apparent lack of impermeability of the fur could be observed in several species of hominoids. For example, in early experiments with a gibbon in a pool it was observed that the gibbon's "thick long wool rapidly became water soaked" (Carpenter 1941, 79). My own

observation and video footage of the common chimpanzee Cooper and the orangutan Suryia during diving behaviour showed that virtually no air was trapped in their fur. Although this feature alone can hardly account for the loss of instinctive swimming ability in apes, it is possibly one of the factors involved in an incipient reluctance to enter water in a common ancestor of all extant hominoids.

To conclude, the common opinion that apes are not able to swim due to an anatomical barrier is clearly rejected here. Further data are needed to assess the variety of swimming patterns in apes and the influence of environmental factors and social learning processes in the acquisition of this behaviour. The Saci LCA hypothesis on the loss of instinctive swimming in this group shall supply an initial framework for the articulation of behavioural, ecological, and evolutionary perspectives related to water use by extinct hominoids.

6.9 Conclusion

In the present thesis different topics related to comparative methods and palaeoanthropological hypotheses were reviewed. The use of convergence as a tool in functional analyses has been discussed, with a special focus on comparisons using distantly related species. Guidelines for this "convergence approach" were formulated and applied in the evaluation of selected hypotheses on the contextualization of early hominins. Additionally, comprehensive reviews on water use in primates were carried out, with a special focus on hominoids, including humans. The first description and video footage of swimming and diving behaviour in a common chimpanzee and an orangutan was offered, along with a description of swimming behaviour in other great apes, with no video footage. Hypotheses on the loss of instinctive swimming in hominoids were discussed and a new model (Saci last common ancestor hypothesis) was proposed to contextualize this behavioural trait (Bender & Bender 2013). Additionally, a hypothesis on the emergence of habitual bipedalism in early hominins was outlined. It was argued that this trait did not evolve in association with a locomotory advantage or otherwise as usually presented in the literature, but as a signal to advertise unprofitability – as a warning signal in an anti-predator strategy. This hypothesis is presented as an example of a model that cannot be evaluated with fossil evidence, but only through comparative data on convergent traits in other organisms which developed aposematism. Consequently, it was argued that fossil evidence does not allow a high resolution of inference concerning incipient traits – traits which are not optimized to fulfil a particular function after a functional change.

A surprising result of the review of water use in primates was the hitherto indeterminate extent of the exploitation of aquatic food resources. Further unexpected, was the finding that great apes often used tools in their interaction with water or used water as a "tool", for example, to drown other individuals. Especially interesting is the fact that some apes understand how to use floation devices and have employed them to escape regularly from islands where they were kept in zoos or sanctuaries. Although this statement might sound paradoxical, I suggest including the theoretical possibility of early hominins as being equally able to use such simple tools and devices in interactions with water. The concept with respect to pre-Oldowan non-lithic material cultures has been explored by Panger and colleagues (Panger *et al.* 2002).

The term "paradoxical" refers to the assumption that a hominin unable to swim instinctively would not be expected to understand the use of primitive floating devices. However, it is argued here that exactly such a non-swimming primate would have greater opportunity to discover the use of such natural devices. As the review on water use in apes showed, the individuals that discovered and used floating devices were not able to swim and were exposed to a high risk of drowning.

In the present thesis theoretical, historical and empirical evidence were considered. To facilitate reading, most historical investigations were placed in an Appendix and referred to them in the main text when appropriate. The historical development of several hypotheses on early hominin evolution was reviewed, for example, the savannah hypotheses and some alternative models, with special focus on aquatic hypotheses. The review of the savannah hypotheses is the first published investigation of the historical roots of this model (Bender *et al.* 2012); this was Professor Phillip V. Tobias' final (or among the last) publications. He – my principal supervisor for this thesis – unfortunately passed away during the printing of this paper. In a further review presented in the discussion of this thesis, it was pointed out that the savannah and other models have similar methodological flaws in the use of analogies to corroborate specific arguments.

In the review of the role of convergence in early natural history I came to an unexpected conclusion. The misinterpretation of convergent organisms played an essential role in the emergence of the first evolutionary ideas in the 18th century by Benoît de Maillet. After an extensive review of de Maillet's ideas and their reception, a re-evaluation of the influence of

this author in the popularization of evolutionary thinking in the 18th and early 19th centuries was proposed. Conclusive evidence that Charles Darwin knew of de Maillet's evolutionary ideas was presented here; specific parts of de Maillet's book *Telliamed* that Darwin marked in his copy were listed. De Maillet should be considered as the first author to point out the medical relevance of water use in humans in an evolutionary framework.

The consideration of different lines of evidence presented in this thesis indicate that the topic "water use" must be considered in discussions on early hominin evolution. Since among hominoids, only humans interact with water in a way that often leads to the development of swimming and diving ability, this can be considered as indicative that at some point in human phylogeny following the hominin/panin split swimming and diving ability may have been specifically selected. However, this assumption is not meant as dogmatic. It is conceivable that our ability to learn to swim and to dive is associated to our cognitive and behavioural abilities and is not a product of specific selection in our past. It is suggested here keeping both alternatives as valid and equal as long as no further evidence on the subject allows a more specific conclusion. Furthermore, it is suggested here investigating water use in primates not as a continuation of the discussion "savannah versus aquatic hypotheses". Although several interesting arguments were proposed in this debate and authors like Max Westenhöfer, Alister Hardy, Elaine Morgan and others have to be acknowledged for their contribution to palaeoanthropological discussion, several arguments pro and con the aquatic models are characterised by dogmatic views, a lack of empirical evidence and a tendency to oversimplify the complexity of this topic. The present thesis shall contribute to restart this research field. I propose to carry out further investigations strongly focussed on evidence and to formulate hypotheses characterised by low degree of speculation and with clear predictions on future findings. To improve methodology in using analogies and in formulating new hypotheses, I suggested using the guidelines of the convergence approach.

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