

**ECOLOGY RESEARCH PROGRESS**

**SEBASTIÁN I. MUÑOZ**  
**EDITOR**

**Nova Science Publishers, Inc.**  
*New York*

Copyright © 2007 by Nova Science Publishers, Inc.

All rights reserved. No part of this book may be reproduced, stored in a retrieval system or transmitted in any form or by any means: electronic, electrostatic, magnetic, tape, mechanical photocopying, recording or otherwise without the written permission of the Publisher.

For permission to use material from this book please contact us:  
Telephone 631-231-7269; Fax 631-231-8175  
Web Site: <http://www.novapublishers.com>

#### NOTICE TO THE READER

The Publisher has taken reasonable care in the preparation of this book, but makes no expressed or implied warranty of any kind and assumes no responsibility for any errors or omissions. No liability is assumed for incidental or consequential damages in connection with or arising out of information contained in this book. The Publisher shall not be liable for any special, consequential, or exemplary damages resulting, in whole or in part, from the readers' use of, or reliance upon, this material. Any parts of this book based on government reports are so indicated and copyright is claimed for those parts to the extent applicable to compilations of such works.

Independent verification should be sought for any data, advice or recommendations contained in this book. In addition, no responsibility is assumed by the publisher for any injury and/or damage to persons or property arising from any methods, products, instructions, ideas or otherwise contained in this publication.

This publication is designed to provide accurate and authoritative information with regard to the subject matter covered herein. It is sold with the clear understanding that the Publisher is not engaged in rendering legal or any other professional services. If legal or any other expert assistance is required, the services of a competent person should be sought. FROM A DECLARATION OF PARTICIPANTS JOINTLY ADOPTED BY A COMMITTEE OF THE AMERICAN BAR ASSOCIATION AND A COMMITTEE OF PUBLISHERS.

#### LIBRARY OF CONGRESS CATALOGING-IN-PUBLICATION DATA

Ecology research progress / Sebastián I. Muñoz (editor)

P. cm

Includes index.

ISBN-13: 978-1-60021-807-1 (hardcover)

ISBN-10: 1-60021-807-5 (hardcover)

1. Ecology--Research. I. Muñoz, Sebastián I.

QH541.2.E255 2006

577--dc22

2007033450

Published by Nova Science Publishers, Inc. • New York

## CONTENTS

<b>Preface</b>	vii
<b>Expert Commentary: New Directions in Palaeoanthropology</b> <i>Marc Verhaegen and Stephen Munro</i>	1
<b>Chapter 1</b> Ecology for Management: Pattern-based Policy <i>Andrea Belgrano and Charles W. Fowler</i>	5
<b>Chapter 2</b> Responses of Microbial Populations and Processes to Pulses of Precipitation in Semiarid Forest Ecosystems <i>Victor Resco and Angel Ferrero-Serrano</i>	33
<b>Chapter 3</b> The Role of Atmospheric N Deposition in Soil Acidification in Forest Ecosystems <i>Yong Sik Ok, Scott X. Chang and Yongsheng Feng</i>	47
<b>Chapter 4</b> Using Bugs (Hemiptera) as Ecological and Environmental Indicators in Forest Ecosystems <i>M. L. Moir and K. E. C. Brennan</i>	79
<b>Chapter 5</b> Effect of Parent Material and Pedogenic Processes on the Distribution, Form and Dynamics of Organic Carbon in Forest Ecosystems in NW Spain. A Biogeochemical Approach <i>M. Camps Arbestain, R. Pardo-Lorenzo, A. González-Arias, S. Virgel, M. Anza and F. Macías</i>	117
<b>Chapter 6</b> The Original Ecomiche of the Genus <i>Homo</i> : Open Plain or Waterside? <i>Marc Verhaegen, Stephen Munro, Mario Vaneechoutte, Nicole Bender-Ose and Renato Bender</i>	155
<b>Chapter 7</b> Soil Engineers as Ecosystem Heterogeneity Drivers <i>Pascal Jouquet, Jérôme Mathieu, Sébastien Barot and Chutinan Choosai</i>	187
<b>Index</b>	199

## PREFACE

The new book presents important recent research on ecology which is the study of the interrelationships between organisms and their environment, including the biotic and abiotic components. There are at least six kinds of ecology: ecosystem, physiological, behavioral, population, and community; specific topics include: Acid Deposition, Acid Rain Revisited, Biodiversity, Biocomplexity, Carbon Sequestration in Soils, Coral Reefs, Ecosystem Services, Environmental Justice, Fire Ecology, Floods, Global Climate Change, Hypoxia, and Invasion.

Chapter 1 - The ecological sciences provide a wealth of scientific information useful for setting policy and establishing management practice. The abundance of publications produced by ecologists contain various explanations of observed phenomena, identification of problems (often global), and descriptions of relationships and patterns in various biotic systems. It is this latter discipline, especially the descriptions of patterns in ecological relationships, that provides realistic guidance for decision-making. The other aspects of ecological science, while not directly useful in management, are relevant, in part because they contribute to our understanding of how patterns serve to guide management – management wherein the subjects of study of these other components of the ecological sciences are themselves taken into account. Patterns are defined herein as sets of information that by abundance and repetition identify limits to natural variation thereby differentiating normal and from pathological. Such patterns are exemplified by macroecological patterns. Normal cases exemplify sustainability compared to cases that are abnormal or pathological and unsustainable under the same circumstances. For example, patterns in predator-prey relationships among non-human species can be used to establish sustainable levels of resource use by humans; patterns in selectivity by non-human species can be used to implement evolutionarily enlightened management through selectivity by humans that mimics the selectivity of non-human species.

This chapter illustrates the use of patterns to establish sustainable harvests (consumption) from ecosystems, from individual species, and from groups of species. Other patterns illustrate sustainable allocations of harvests among alternative species. Still others illustrate the advisable size for protected areas along with their optimal locations. The authors chapter specifies the best science for management (and specifically for ecosystem-based fisheries management): the science that characterizes patterns that are integrative of complexity through the processes and factors that contribute to their origin – their emergence. More precisely, this science provides characterization of patterns that are consonant or isomorphic

with the specific management questions being addressed. This is in contrast to the current use of scientific information. In conventional management, the ecological information we choose for determining management policy demands, and relies on, non-objective opinion and mistranslation of piecemeal information – often as patterns, but rarely consonant with management questions. The human conversion of non-consonant information to consonant information of conventional management is to be contrasted with the consonance of patterns that require no conversion in systemic management. In this way, systemic management, as pattern-based management, is objective, consistent, and widely, if not universally, applicable.

Chapter 2 - Understanding how abiotic factors regulate soil microbial activity is key in understanding the responses of terrestrial ecosystems to anticipated climate change. Soil microbes catalyze biogeochemical reactions and the exchange of nutrients between heterotroph and autotroph organisms, as well as between the soil and atmosphere. Semi-arid forests are driven by "pulses" of precipitation (episodic and irregular events of precipitation) which activate soil microbial activity and their processes. Our knowledge on the functioning of semi-arid forest ecosystems in response to pulse events has increased substantially over the last decade. However, a comprehensive paper synthesizing this literature and making conceptual progress at global scale is yet missing. This paper is a review of the current knowledge on microbial populations and their processes in forest semi-arid ecosystems after pulse events. First, the authors briefly describe distribution and abundance of soil microbial biota in these systems. Second, the authors review ecosystem processes, and how they are regulated by microbial communities. These ecosystem processes include soil respiration, carbon and nitrogen dynamics and decomposition. Third, the authors address the effects that climatic change may exert on these populations and processes. The effects described are increased CO<sub>2</sub> concentrations, elevated temperatures and changes in precipitation regimes.

Chapter 3 - The emissions of NO<sub>x</sub> and NH<sub>3</sub> into the atmosphere are on the rise, and the emitted N compounds are distributed globally, causing concerns over possible effects on human health and the environment. The emission of N occurs primarily from agricultural activities and fossil-fuel combustion (e.g., automobile and industrial boilers). Atmospheric N deposition has become an important factor affecting forest health and sustainability in recent decades, partly as a result of decreasing S emissions. Nitrogen compounds that fall onto soil and water bodies with precipitation and dry deposition can cause damage to ecological systems. Chronic excessive N input can lead to base cation depletion, nutrient imbalances, eutrophication, soil acidification, and forest dieback. Leaching losses of NO<sub>3</sub> gradually decrease the acid buffering capacity of forest soils. Moreover, releases of Al and Mn induced by soil acidification cause toxicity to trees. Biological processes play a crucial role in soil acidification, as N compounds originated from atmospheric deposition undergo nutrient cycling processes. However, the effects of N transformation on soil acidification in forest ecosystems are often overlooked. Thus, an improved understanding of the impact of atmospheric N deposition on N cycling processes is needed to better predict the responses of forest ecosystems to such depositions. In this paper, the authors explore the linkage between N cycling and soil acidification in forest ecosystems, and evaluate the role of N cycling and atmospheric N deposition on soil acidification in forest ecosystems by discussing: 1) the N cycle and its effect on soil acidification in forest ecosystems, 2) the effect of N deposition on forest soils and trees, in terms of base cation depletion, soil acidification, and aluminum toxicity, 3) leaching losses of N from forest soils, and 4) critical loads of atmospheric N deposition in forest ecosystems.

Chapter 4 - Many orders and families of invertebrates have been promoted as ecological and environmental indicators of management practices and natural disturbances in forest ecosystems. To date most research has focused on ants, particularly for gauging the success of efforts to restore lands modified by human disturbance. However, it is now recognised that a range of taxa are potentially required. Here, beetles, butterflies, ants and spiders have received interest as potential candidates for the 'shopping basket'. Less well known, but of great importance, are responses by the hyperdiverse order Hemiptera (true bugs). Recent research along a latitudinal gradient shows Hemiptera to be one of the best orders of invertebrate at discriminating between different forest types. This paper reviews the benefits of incorporating Hemiptera into ecological studies examining forest management practices. The authors describe the contribution Hemiptera make as the fifth most speciose insect order to forest biodiversity, their functional role in ecosystems, and their role as forest pests. Hemiptera occur in all forest strata (e.g., soil, leaf-litter, understorey, overstorey). As abundant and diverse prey they are likely to contribute to the high diversity of other arthropods plus insectivorous birds, mammals and reptiles. Although most Hemiptera are herbivorous, the group exhibits a wide spectrum of feeding habits, including predators, fungivores, and parasites. Even within the herbivores there is great variation owing to different host specificity levels, with some species highly monophagous (feeding only from one species of plant), through to species that are highly polyphagous (feeding from different families of plants). As many polyphagous Hemiptera often target plants with high nutrients, individual plants within a species may also differ in their hemipteran assemblages owing to differences in nutrients. This diversity in trophic requirements means that Hemiptera are sensitive to changes not only in habitat structure, but also floristics and changes in plant chemistry. Similarly, seasonal changes can also influence the structure of hemipteran assemblages at spatial scales ranging from individual plants up to forest plots. The authors review the most efficient methods for sampling Hemiptera, for example, beating, pitfall traps, vacuum sampling, intercept traps and chemical knockdown. The authors examine current knowledge on the response and recovery of Hemiptera to different forest disturbances, such as fire, fragmentation, windthrow, disease and flood. The authors then illustrate these points by summarizing studies in a forest system being restored following the severe disturbance of mining. Finally, the authors detail the role that both introduced and native species of Hemiptera display as pests in forest or silvicultural systems, as outbreaks of Hemiptera can indicate when a system is stressed, particularly by drought or flooding.

Chapter 5 - The main objective of the present study was to determine the effect of the type of pedogenesis generated by two different parent materials – amphibolite (AMP) and granite (GR) - and the effect of different forest stands - pine (P), eucalypt (E), and oak (O) - on the quality and quantity of organic C pools in udic, mesic and freely drained systems. Five C pools were studied: aboveground biomass, belowground biomass, dead wood, litter, and soil organic matter (SOM) in the Ah horizons. The three forest soils derived from AMP materials (AMP-P, AMP-E, AMP-O) were classified as Typic Fulvudands and Aluandic Andosols, and the three forest soils derived from GR rocks (GR-P, GR-E, GR-O) were classified as Humic Dystruddepts, and Leptic and Haplic Umbrisols. All soils are located in the surroundings of Santiago de Compostela (A Coruña, NW Spain), where the mean annual air temperature is 12.3 °C and the total annual precipitation is 1624 mm yr<sup>-1</sup>. The results obtained indicate that highest total organic C stocks in the ecosystems studied (down to the lowest depth of the Ah horizons), i.e., the sum of the five reservoirs considered, always corresponded

to the eucalypt stands, with stocks  $> 500 \text{ t ha}^{-1}$ , whereas those of the oak and pine stands were always  $< 500 \text{ t ha}^{-1}$ . The mean distribution of organic C stocks in the five reservoirs considered was as follows: aboveground biomass, 18.4%; belowground biomass 4.6%; dead wood, 1.1%; litter 8.4%; and soil organic C, 67.2%; there were no significant differences ( $P < 0.05$ ) between means of the AMP and GR ecosystems although the total C stocks were always higher in the AMP than in the GR ecosystems, and followed the order  $E > P > O$  in both. There were significant differences ( $P < 0.05$ ) in the quantity, quality and dynamics of organic C in the two types of ecosystems, when organic layers (L and F) and also Ah horizons (Ah1 and Ah2) were distinguished, as discussed below.

The results indicate that, in soils developed from GR, the lithology mainly determines the type of pedogenesis taking place in the surface horizons, with intense acidification (acid-complexolysis) associated with scarce or nil neof ormation of secondary minerals in the most acidic compartments (L and F layers) and an abundance of aqueous and mobile organo-metal complexes. Under such conditions, decomposition of primary OM is very slow, leading to the accumulation of undecomposed debris in the organic layers. In soils developed from AMP, both lithology and plant species clearly affected pedogenesis in the surface horizons. Surface acidification occurred in the pine stand (although never as intense as that occurring on GR materials), but greater than that of AMP-E and AMP-O litters. In general, the more eutrophic conditions of the AMP soils, compared with the GR soils, appeared to allow rapid decomposition of primary OM. The geochemical conditions of the AMP Ah horizons also appeared to allow neof ormation of metastable forms of gibbsite and different short-range order 1:1 aluminosilicates able to bind to secondary organic compounds. Under such conditions, decomposition of secondary OM was probably preserved, as reflected by the high organic C content of the Ah horizons. All of this may explain the existence of a moder-type OM in the GR soils, in comparison with the Al-mull type form of the AMP soils. Overall, the results obtained indicate that parent material affects the distribution within the soil profiles studied, as well as on its quality and dynamics within the soil profiles studied, whereas the organic C stocks present in the aboveground biomass were more affected by the type of forest species and management.

Chapter 6 - That humans evolved as a result of a move from forests to more open plains is still the prevailing paradigm in anthropology, and researchers often assume that this transition influenced the origins of human bipedalism, omnivory, tool use, large brains, and even speech. Here, the authors argue that there are no scientific grounds on which to base such a hypothesis. While we agree that *Homo* may have evolved in more open (tree-poor) habitats than other apes (which could account for our relatively poor climbing skills), the suggestion that humans shifted to drier habitats away from water is, according to our research, unproven. The authors propose instead a more parsimonious model compatible with all known data and corroborated by a number of independent sources of evidence.

Comparisons of the locomotor styles and nutritional requirements of extant species and anatomical comparisons of fossil and extant species including *Homo sapiens*, especially in the combination with palaeoecological data, strongly suggest that early *Homo* evolved at the water's edge (whether in savannahs or elsewhere) where resources essential for brain growth were both abundant and easily procurable by a thick-enamelled tool-using omnivorous hominid.

Chapter 7 - Ecosystem engineers function as regulators of ecosystem functions by influencing the fluxes of energy and materials across different spatial and temporal scales.

Understanding how ecosystem engineers affect the dynamic of heterogeneity in ecosystems is becoming a fundamental component of both theoretical and applied Ecology. This manuscript offers a conceptual discussion for characterizing how and why soil engineers (earthworms, termites and ants) affect heterogeneity patterns.

There are two types of ecosystem engineers in soils. Extended phenotypic engineers concentrate their activities on the building of biogenic structures (earthworm casts, galleries and nest structures) in order to maintain optimal conditions for their growth. Conversely, accidental engineers expend energy in moving through the soil to find their optimal environment. Although both types of engineers create patches in an ecosystem, the authors argue that extended phenotypic engineers have more effects on ecosystem heterogeneity since their activities are more concentrated in space, as compared to accidental engineers, which move and contribute to homogenisation of ecological processes throughout the whole ecosystem. Finally, the authors discuss how soil engineers affect ecosystem processes (e.g., carbon, water, and nutrient cycling) at higher scales than those of their own functional domains. While some biogenic structures can be looked on as patches or hot-spots without any interactions with their neighbourhoods at small space scales, others interact and constitute gradients and networks that significantly affect ecosystem processes, such as the population dynamic of trees or soil erosion at the landscape scale.

The authors argue that it is necessary to have a quantitative knowledge on the size, boundaries and dynamics of patches created by soil engineers. Embracing the links between the ecology of engineers and the frontiers of their sphere of influence will enhance understanding how spatial heterogeneity regulated by ecosystem engineers affect pools and fluxes in ecosystems.



*Expert Commentary*

## NEW DIRECTIONS IN PALAEOANTHROPOLOGY

**Marc Verhaegen\***

Study Center for Anthropology, Mechelbaan 338, 2580 Putte, Belgium

**Stephen Munro**

School of Archaeology and Anthropology, Australian National University, Canberra,  
ACT, 0200, Australia

Anthropology, a specific subfield of ethology, because it deals specifically with our own species, tends to be characterized by a more emotional approach than is common in other ethological fields. This may explain why standard methods that are commonly used in ethology, such as comparative biology, are remarkably rare in anthropology and especially palaeoanthropology. Anthropologists tend to view humans as unique, and therefore fail to apply comparative methods on humans and their fossil and living relatives, as would be done as a matter of practice in a number of other fields. As long as this anthropocentric attitude continues, it will remain impossible to reconstruct human evolution in an objective manner.

It is now more than half a century ago that Max Westenhöfer (1942), and later Sir Alister Hardy (1960), proposed on the basis of comparisons with other animals that humans were more aquatic than had generally been accepted. They had noticed (independently) that humans differ from other primates by possessing a much thicker layer of fat directly under the skin, and by lacking fur on most parts of their body. To them, this was a striking similarity to other furless mammals with high amounts of subcutaneous fat. All mammals that are both fat and naked are either fully aquatic or tropical semi-aquatic (the reverse does not necessarily hold), for instance, the Sirenia, Cetancodonta (whales, dolphins and hippopotami) and some Suidae and Pinnipedia. Since this is the case, why should humans be an exception? When Hardy (1960) straightforwardly suggested that this might point to a semi-aquatic past for our ancestors in tropical regions, he was either ignored or ridiculed by nearly all anthropologists. It was then believed (for reasons we describe in Chapter 6, "The original econiche of the genus *Homo*: open plain or waterside?") that humans had evolved directly from forest dwellers (quadrupedal non-human primates) to become open plain dwellers (bipedal humans). The fact that other primates that went from forests to open plains, such as savannah baboons, had not lost their fur, had not developed large subcutaneous fat tissues, and had in

---

\* marc.verhaegen@village.uu.net.be

fact become more quadrupedal rather than bipedal, was and still is apparently of no concern for those favouring the 'quadrupedal = forest, bipedal = open plain' model.

Whenever fossils of possible human relatives are found, the palaeofauna and -flora tend to be viewed in light of the open plain interpretations, and most interest therefore focuses on whether the landscape was open or forested. The fact that aquatic taxa are prevalent at many sites (see Chapter 6) seems inconsequential, and these are usually only referred to in scientific papers if they add something to the dating, stratigraphy or taphonomy. This unbalanced focus can be explained by the implicit or explicit conviction that the open plain or savannah view of human evolution is beyond doubt, an attitude which we think is largely due to a combination of educational biases and anthropocentrism. It is difficult to understand, for example, that anthropologists rarely consider the obvious fact that what is true for other animals (for instance, "all fat and naked mammals spend a lot of time in the water") might also be true for human ancestors.

It is clear to us that a reconsideration of the usual anthropological models for human evolution without anthropocentric biases will open new insights into how our ancestors evolved. In Chapter 6, we first reconsider the 'open plain' idea by examining one of its most recent incarnations, the 'endurance running' model, and show by using objective criteria such as comparative data that there is no support for a savannah or endurance running based interpretation of our past evolution. We then reconsider the sites of fossil *Homo* in an unbiased way, and conclude that most if not all sites were clearly at the waterside.

In our opinion, the reconstruction of the evolutionary history of a living species should be based in the first place on behavioural, anatomical and physiological comparisons of the species to its extant relatives and to other animal species, rather than on the interpretation of fossil finds. This is primarily because making sense of the (usually patchy, incomplete and scanty) fossil record strongly relies on interpretations, and it is never certain whether the supposed ancestor was an evolutionary dead end or really was an ancestor of a living species: we know we had ancestors, but we do not know whether fossils have descendants. At the same time we think that anthropologists need to acknowledge how unlikely it is that human subcutaneous fat, furlessness, breath-hold capacities and poor olfaction could have evolved because human ancestors lived in dry, open habitats.

We suggest two methods should be employed more frequently for future research into reconstructions of how human ancestors may have lived:

- (1) In describing the accompanying palaeoflora and -fauna of a hominid site, attention is often given to the larger mammals and to the animals that can be thought to elucidate the supposedly savannah lifestyle of our ancestors. We suggest that the invertebrate, fish, avian, reptilian and smaller mammal fauna should also be studied in detail, and that anthropologists should keep an open mind to the possibility that not only the savannah itself, but the waterside, whether in the savannah or not, might be an essential element in human and hominid evolution. It is true that fossilisation in terrestrial settings mostly occurs in sedimentation in quiet waters and that this alone by no means suggests that the animals fossilised lived in these waters, but it is also the case that this does not exclude the possibility that they might have spent more or less time in these waters. Preliminary (Verhaegen and Puech 2000) and more thorough studies (Munro 2004, and Chapter 6 in this book) of the fauna associated

with hominid palaeoenvironments reveal that the aquatic components are often both significant and considerable.

- (2) Anthropologists who construct models of the original human eoniche tend to focus on the fossil evidence. But while the fossil record can provide crucial insights, its importance can also be overstated. Fossils are incomplete, typically they are fragmented pieces of bone without soft parts, and their exact phylogenetic relationship to living species is often uncertain. Frequently, species, age and sex are unknown, and the geological age and palaeoenvironment uncertain. The comparative method, which compares the behaviour, anatomy, physiology and DNA of *living* animals, is more secure, systematic and reliable than the fossil evidence. Therefore, we think thorough inventories and comparisons of the most diverse features of the most diverse animals are needed in order to discover correlations between these features.

Human features such as language and bipedal locomotion are often seen as unique, and consequently anthropologists tend to rely on functional interpretations instead of comparative arguments. But functional interpretations often mean subjective 'explanations': since we 'know' our ancestors lived on the savannah, it is easy to conclude that in humans, unlike savannah mammals, the function of subcutaneous fat, for example, was for thermal insulation in the cool savannah night, or as an energy depot to combat extended dry seasons. And because it is 'known' human ancestors were living on the savannah, there is no need to consider that subcutaneous fat, seen in all fully aquatic and many part-time water dwelling mammals but never in typical savannah mammals, could have been an adaptation to part-time water dwelling (be it for energy storage, thermo-insulation, streamlining, buoyancy or some other reason).

That some human features can appear to be unique, such as our language and locomotion, does not mean that comparisons with other animals can not be made. What is required is to separate these features into as many individual components as possible (ideally these components should be independent from each other). The finer the distinctions, the more detailed reconstructions can be obtained. Since biological features are generally inherited independently of each other (Mendel's Laws), due to the crossing-over and re-assortment of chromosomes during meiosis, there is no reason not to use an analytic approach.

We provide a possible illustration as a starting-point for future research. It is often believed that human locomotion was an adaptation to the open plains, but when we separate our locomotion into its individual elements, this belief appears to be a just-so interpretation:

- a) *two-leggedness* is seen in birds (including ostriches, flamingoes and penguins), many dinosaurs, and diverse mammals (including hopping mice and kangaroos on the savannah, indris and gibbons in the branches, and lowland gorillas and proboscis monkeys while wading, though not in most wading mammals);
- b) *full plantigrady* (with the heels usually touching the ground or branch) is, for instance, seen in water opossums and sealions, whereas cursorial animals run on their toes or hooves (digit- or unguligrady);
- c) *very long legs* relative to trunk length are typical of frogs, kangaroos, indris, tarsiers, giraffes, ostriches and flamingoes, to name a few;

- d) *straight legs* (as opposed to bent-knees-bent-hips in rest) are seen from wading-birds to giraffes, especially in large and heavily-built species;
- e) *a striding gait* (with alternating limbs, as opposed to hopping) is seen in many walking, running and wading birds, and more frequently in larger-sized than in smaller birds;
- f) *truncal erectness* is seen in some arboreal species (especially tarsiers and gibbons), meerkats on the look-out, penguins on land, etc.;
- g) *a latero-laterally broad trunk* is typically seen in beavers and platypuses, and to a lesser degree in brachiating primates (apes and atelids);
- h) *an alined body* (with head, trunk and legs in one line) is typical of swimming animals; and so on.

While we realise that these resemblances are often subjective and that the comparisons are preliminary, they nevertheless indicate that humans resemble cursorials (c) less than they resemble arboreals (c, f), waders (c, d, e) and swimmers (b, g, h). This would be consistent with an idea that human ancestors were once tree dwellers who learnt to wade, swim and run.

This exercise can be repeated with all other features in which humans differ from our closest relatives the chimpanzees: furlessness, subcutaneous fat, olfactory reduction, external nose, parabolic tooth row, very large brain, and even human speech can be analysed into smaller elements (Verhaegen and Munro 2004). By combining all these results, we can develop a data set that can be used to evaluate various models of human evolution, including the 'waterside' and 'open plain' models.

In our opinion there has been too much focus on the role of open plains in human evolution, and not enough consideration given to the role of waterside habitats. Decisions of which data to collect and which models to test are compromised because of a widespread acceptance within the anthropological community that human evolution took place on the savannah. To redress this imbalance and to ensure a more objective approach, we believe that the study of how human ancestors lived will be greatly improved by (1) a non-savannah focused reconsideration of the fossil palaeoenvironment, and even more so by (2) a detailed and analytical comparison of typical human features with the widest possible range of animals.

## REFERENCES

- Hardy, A. (1960). Was man more aquatic in the past? *New Scientist*, 7, 642-645.
- Munro, S. (2004). *Fauna of Selected Late Miocene to Early Pleistocene Fossil Sites* (BA Honours thesis). Canberra: Australian National University.
- Verhaegen, M., & S. Munro (2004). Possible preadaptations to speech – a preliminary comparative approach. *Human Evolution*, 19, 53-70.
- Verhaegen, M., & P.-F. Puech (2000). Hominid lifestyle and diet reconsidered: paleo-environmental and comparative data. *Human Evolution*, 15, 175-186.
- Westenhöfer, M. (1942). *Der Eigenweg des Menschen*. Berlin: Verlag Die Medizinische Welt.