Ole Seehausen

LAKE VICTORIA
ROCK CICHLIDS

— taxonomy, ecology, and distribution —

VERDUIJN CICHLIDS

Lake Victoria Rock Cichlids

Lake Victoria Rock Cichlids

— taxonomy, ecology and distribution —

by

Ole Seehausen
Institute of Evolutionary and Ecological Sciences,
University of Leiden, Netherlands

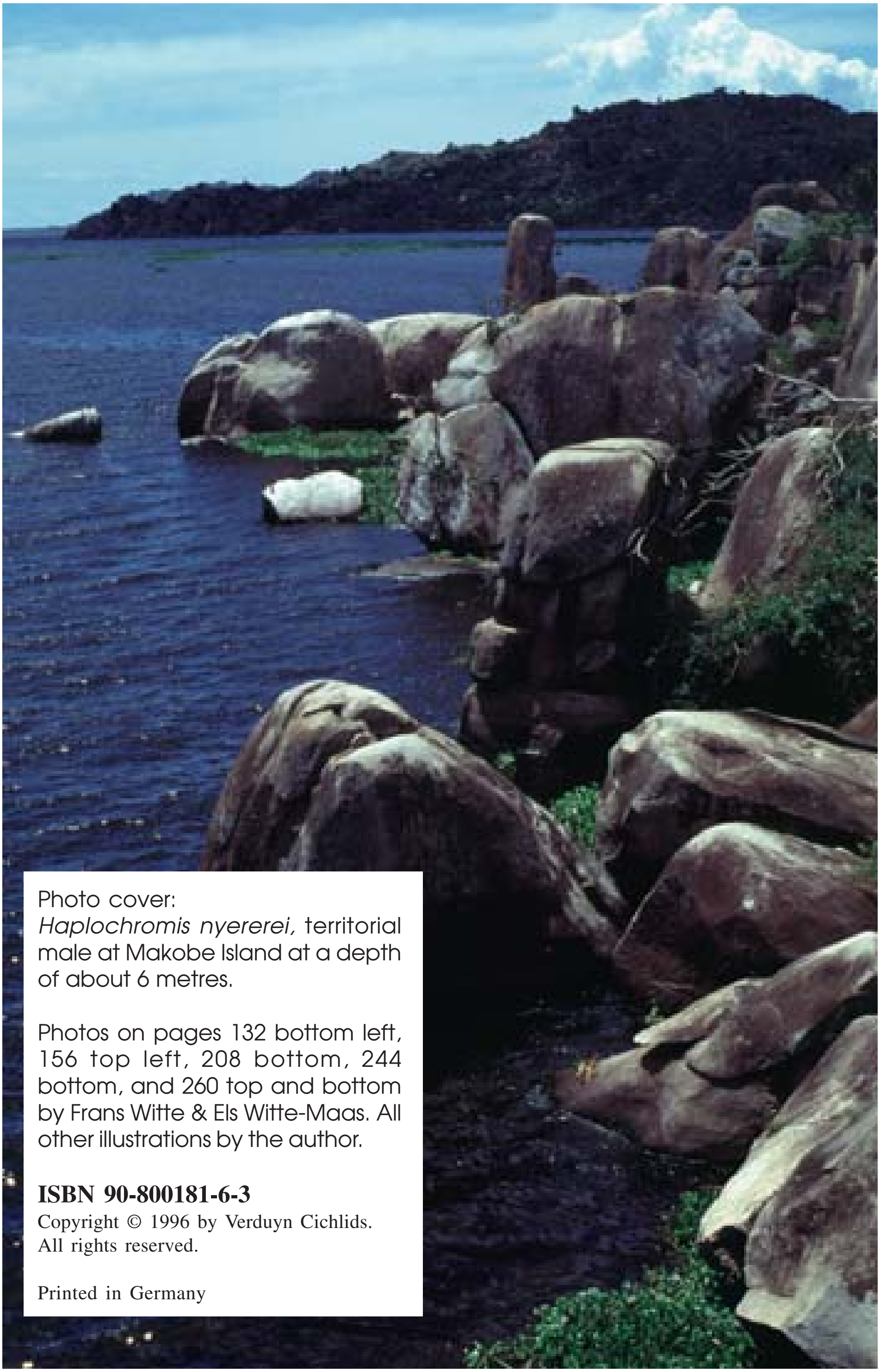


Photo cover:
Haplochromis nyererei, territorial male at Makobe Island at a depth of about 6 metres.

Photos on pages 132 bottom left, 156 top left, 208 bottom, 244 bottom, and 260 top and bottom by Frans Witte & Els Witte-Maas. All other illustrations by the author.

ISBN 90-800181-6-3

Printed in Germany

Contents

Rock-dwelling species of other lineages

Preface

Professionals and amateur students of aquarium fishes both begin with joyous, boundless enthusiasm, but things have a way of getting too serious in the pro world, and the fun starts to slip away. For those of us who work on cichlids from East Africa, the fun really started wearing thin sometime in the late 1980s, when it became apparent that several hundred species of cichlid fishes from Lake Victoria that hardly anyone had ever seen, might never be seen again. The world's second richest lacustrine fish fauna had been destroyed by humans mucking about, reorganizing things so that the lake could produce fish more marketable overseas. Hundreds of fishes extinct, but then again, hundreds of millions of dollars per year pumped into one of the neediest regional economies in the world. A Faustian compromise if ever there was one.

Someday there could be an inspiring movie or television show made about the group of scientists from Africa, who along with their colleagues from Europe, the Middle East, and North America, got together to save their beloved lake from Nile perch, pollution, water hyacinth, and all the other symptoms of the suffocating pressure of humanity. They got the data, blew the whistle, got into trouble with authorities, worked hard, raised money, fought over money, sued each other, died, had kids, and generally shared two decades of the joys and tragedies of East Africa. Through it all they learned a whole lot about each other, and about life. Meanwhile, the East African Community, left in tatters in the wake of Idi Amin, was awoken from its deep slumber, in good part by embarrassment (and an embarrassment of international funding and publicity) over the state of Lake Victoria. Yet, almost lost in the shuffle were the haplochromines themselves... those beautiful, fascinating, and economically almost worthless little fishes that started it all by checking out en masse.

If the shattered remnants of bombed-out Nature would just fade quietly into the realm of paleontology, biologists would be able to savor their grief without ever having to worry about social responsibility. That isn't how it happened in Lake Victoria. Large chunks of the native fauna just hung on. A few species are even resurging in abundance now that the famed Nile perch is petering out a bit. Included among these are the magnificent fauna described in this book. These may be the most beautiful, abundant, and easily located vertebrates to have escaped the notice of people for this long. They've got the Vietnamese bovids beat hands down.

How could more than 200 species of conspicuous aquatic vertebrates crowd the shallow waters of the earths' second largest lake, yet go unnoticed through most of the 20th century? Perhaps the same way that an equal number could vanish completely from these same waters, within a period of only five or six years, yet inspire barely an epitaph save for the sorrow and disappointment of a handful who knew and understood. Other than the African and visiting scientists who have borne witness to these events firsthand, nobody could feel the full loss. But if you are one of these scientists or a knowledgeable hobbyist, you should be seething with anger – anger craving a useful and rewarding outlet.

You can't miss something that you never even knew was there. But you cannot save (from our own brutal hand) something that you do not know and love. So, to know and to love, to celebrate and to share, to generate interest and funds to where they are most needed in conservation: that is what aquarists can do to save faraway species from extinction. But to do so you need a primer, a guide. You need the information.

A male Haplochromis "red back scraper" in the aquarium.

sipping fresh beer through long, long straws, and telling rowdy stories. It is maybe eleven at night and dinner is still on the fire. You hear a hyena call, not far away, and then somebody's dog. And what are people talking about? After the stories about who fell out of the boat, or caught the best fish, or made the villagers clutch their sides the laughter was so painful, the conversation shifts to the price of haplochromines on the European marketplace. Or the possibility that a school might be built with

You need the direct contact with your shaman, the aquarist-turned-field biologist. This book is the first specialized guide on any of Lake Victoria's endemic 'treasures written especially for fish knowers and lovers. And Ole Seehausen is a shaman par excellence. So do it. You are the troops, and here are your orders: get to know these little fishes. Keep them in your aquariums, breed them, photograph them, watch them, worship them, in the funny little way we do that nobody else seems to understand. Write about them, talk about them, spread enthusiasm and appreciation, celebrate the fishes, the fauna, the lake, explain your dedication to non-aquarists. Do not let them die – in the wild, or in your hearts and minds. This is your revenge. Do you doubt that what you do can make a difference in the context of a distant, different culture? But then for you, which culture is truly the alien one? The culture of Kampala/Munich/London/New York that exists apart from, and in disdain of, all nature and things wild? Or the culture of the woods and waters everywhere remote, where the last proud remnants of the planet's living wonders quietly await their demise?

If you are reading this book, you needn't even think about your choice. You are one of us. This is your adventure. You are in East Africa, at lake side. It is a dark night, and you are the only foreign visitor amongst your many African friends around the campfire,

the proceeds of aquarium fish sales, right on your campsite, to help people, and to help them know about value, and safeguard their aquatic heritage. About how after a whole day, you finally succeeded in explaining to the local fish collectors (mostly little children) that they should return the young, unsalable fishes alive to the lake instead of tossing them to die up on the grass. How are the kids in Boston, how's so-and-so's health in Leiden, is that fellow's father down in Masaka feeling better? Somebody says to your friend, who is lifting a haplochromine appetizer from out of the coals, "You should have preserved that as a specimen – you cooked a rare fish!" and he answers, "Yes, but I cooked it only briefly... and I will study it internally". During dinner everyone talks with animation about what was learned about the fishes or the lake that day: why it matters, and how best to tell the rest of the world about it. These are your soul mates. This book is, through Seehausen's art, a gift from them to you. It is also your initiation into our circle. Enjoy this book, enjoy the fishes, and then, enjoin the battle to save all living things beautiful, and richly varied, and worthless in the eyes of the ignorant.

Les Kaufman
8 Sept.1996
Boston University Marine Program,
Kenya Marine and Fisheries
Research Institute, and Fisheries
Research Institute of Uganda

Introduction

A number of books have been published during the past years, that dealt with the biology of East African lake cichlids in their natural environment. In this book, I want to pick up that thread. Nevertheless, the book is by necessity quite different from the others. Not only that it is the first popular book about Lake Victoria cichlids, but it reports about a species assemblage that is largely new to aquarists and scientists alike. Of the 173 species discussed in it, merely 34 have been scientifically described yet. The majority of the "new" species were discovered between 1991 and 1996 during the first extensive ecological and taxonomical survey of rocky shores in south-eastern Lake Victoria. They constitute a Mbuna-like species assemblage of Lake Victoria cichlids, that was explicitly believed not to exist! A huge group of probably more than 200 haplochromine cichlid species had simply been overlooked.

All around the world the cichlid faunas of the East African Great Lakes fascinate students of evolution as much as aquarium hobbyists, enjoying and observing the products of evolution. A continuous flow of publications of various kinds results from this fascination. Apart from their enormous diversity in form and coloration, a number of unique features made the cichlids of Lakes Malawi (Nyasa) and Tanganyika famous: One is the highly developed habitat specificity and site fidelity of rock-dwelling

The north-west corner of Gana Island, the most remote locality visited by the author.

cichlids, resulting in unusually high levels of regional and local within-lake endemism and extraordinarily high numbers of species. Another one are the fascinating similarities that evolved among individual rock-dwelling species of Lakes Malawi and Tanganyika as well as among whole communities (Lowe-McConnell 1993).

It has long been believed that highly developed habitat specificity, site fidelity, and restricted distribution within the lake are much more muted, if at all developed among the cichlids of Lake Victoria, and that a species rich rock-dwelling cichlid assemblage would not exist in this lake. Results of more recent research had indicated since the early eighties, that these assumptions might be wrong. The existence of a group of cichlids, very similar to the Malawian *Mbuna*, inhabiting the rocky cliffs in Lake Victoria, was first mentioned by van Oijen et al. (1981). The first cichlid collections at rocky islands in southern Lake Victoria were done in 1978/79 by Els Witte-Maas and Frans Witte, in 1986 by Jan Sevenster and in 1989 by me. In 1990 long term field research on rock-dwelling cichlids was taken up by Niels Bouton and Yves Fermon, and in 1991 by me. Over those years, and in particular during the last five years, a large variety of new species has been discovered. I hope the results of this most recent work on rocky shores will convince most of those authors that until now kept to the old assumptions, when comparing the cichlid flocks of the East African Great Lakes.

In species richness, ecology, morphology and behaviour of the species, the assemblage of rock-dwelling cichlids in Lake Victoria closely resembles that in Lake Malawi. At the time of writing more than 170 haplochromine species are known from rocky substrates in the south-eastern lake region. This has far reaching implications for the interpretation of evolution in Lake Victoria. The "new" cichlid assemblage carries a great potential both for biological research and for the aquarium hobby. Apart from that its role in the ecosystem of the lake needs to be studied. The purpose of this book is to give a first introduction to this overlooked fauna, and to make researchers, hobbyists, and conservationists aware of its riches.

Most emphasis is laid upon the presentation of the various species complexes and species, with much new information about distribution, ecology, and behaviour in their natural environment. For this purpose underwater work by Scuba was done for the first time in Lake Victoria. The lake, widely known as a turbid one, has never attracted diving researchers or cichlid enthusiasts. This is certainly one reason for that its rock-dwelling cichlids were discovered that late. Lake Victoria is indeed turbid compared to Lakes Malawi and Tanganyika. Nevertheless, it is at some places clear enough to study the behaviour and ecology of the cichlids. Much of the new ecological information brought together in this book has been gathered by Scuba. Unfortunately, however, the low water transparency makes photographing much more difficult and less attractive than it is in the clear Lakes Tanganyika and Malawi. Consequently most of the fishes for this book had to be photographed in a photo cuvette immediately after capture.

Apart from harbouring the large assemblage of "new" *Mbuna*-like rock-restricted cichlids, rocky shores and islands are the most important refugium for a number of cichlid species that were formerly not restricted to rocky substrates, but survived only there after the Nile perch upsurge ("rock-refugees"). Many readers may be familiar with what happened in Lake Victoria. The Nile perch (*Lates sp.*), a big predator, was introduced by man in the 1950s. When its numbers increased explosively in the early 1980s, the populations of most open and deep water dwelling cichlid species crumbled. An estimated number of 150-200 endemic cichlid species disappeared, many of which probably went extinct (Witte et al. 1992). The cichlids that inhabit rocky shores and some other littoral habitats were less than others affected by these events. Rocky habitats of Lake Victoria currently prove to be of major importance to the survival of at least some of the endangered species. At present they harbour the largest anatomical, ecological, and possibly genetical diversity in Lake Victoria. This refugium which is dispersed all around and across the lake, may come to play a central role in the further evolution of Lake Victoria cichlids.

The first rock-dwelling Lake Victoria cichlids that became available to aquarists were exported from Uganda in the 1980s. Recently the utilization of rock cichlid populations as source for aquarium fishes is becoming more permanent. Currently at least about 50 species are kept by aquarists. It is likely that in the near future they will become the major source for aquarium fishes from Lake Victoria. Rock-dwelling Lake Victoria haplochromines, if given the publicity, they deserve, are likely to become as attractive to aquarists as *Mbuna* are.

High time therefore, to look at Lake Victoria's rock cichlid assemblage more carefully. I wish this book can make a start in documenting its extraordinary diversity, and lay the ground for further documentation in the natural environment, as well as for identification and documentation of fishes that are being imported to America and Europe in increasing numbers. Because more than 120 species are presented here for the first time in literature, and no other references exist to them, more taxonomical details had to be given in this book than would otherwise be needed in a popular book. It is my hope that the book, nevertheless, makes interesting reading for hobbyists and biologists alike.

It needs to be stressed that the work, the book is based on, is not the work of one person. Rather it is the work of a team of varying composition. I am very much indebted to all members. Those to be mentioned in particular are our boat captain and chief fisherman Mhoja Kayeba who worked with the research teams of Leiden University for more than 15 years, and is probably one of the most skilled boat drivers in the Tanzanian part of Lake Victoria. Apart from his great skills he also contributed to the work a great lot of enthusiasm for the cichlids. Ruben Enoka has always been the chief fisherman in our team. I thank him for many years of excellent collaboration and particularly for solving various kinds of difficulties with great discipline. Anna Samwel-Terry has as field and laboratory assistant been contributing a lot to various kinds of work on the lake and in the laboratory, and concerning this book in particular. She did most of the stomach content analyses of the new species. Hence her contribution to the book goes beyond her co-authorship in the chapter on ecology, and all across the species chapters. I am very much indebted to Mohamed Haluna, Ali Marwa, Masoud Ilomo and Aloys Peter for their expertise as fishermen in cichlid collecting. Radhmina and Gonza Mbilinyi-Kitery, Mr. Mapunda, Kassim Mgady Hamissi, Sylvester Wandera, and John Balirwa are thanked for much logistic and other support. Niels Bouton and Yves Fermon are acknowledged for collaboration and logistical support during my first stays in Tanzania. Both are researching about evolution and ecology of Lake Victoria rock cichlids, and the reader will come across their names here and there in the book. Finally, Frans Witte, Jacques van Alphen, and Kees Barel are greatly acknowledged for a lot of encouragement and scientific advice in our work. Frans Witte read and improved parts of the book manuscript, discussed with me species identifications and made available some of his and Els Witte-Maas' data and photographs. I thank Rob Hoogerhoud for making available his drawings of cichlid jaws, my grandfather Helmut Seehausen for his paintings of cichlids, and Peter Snelderwaard for X-ray photographs and other support.

The book would not have been written without the support of the Tanzanian government. I am grateful to its Commission for Science and Technology for the research permit that allowed me to carry out the work, and to the Tanzania Fisheries Research Institute (Prof. Philip O.J. Bwathondi) for accommodating my research. Egid F.B. Katunzi, as the director of the Mwanza centre of TAFIRI deserves particular mentioning for his and his staffs' hospitality and support during my ongoing studies. I am grateful also to the Ugandan Fisheries Research Institute (FIRI) in Jinja for their hospitality and support during my short visit in 1989. The research, of which this book is a spin-off, was financed by grants from the Netherlands Organization for the Advancement of Tropical Research (WOTRO), the TETRA company (Germany), the EHEIM company (Germany), and the German Cichlid Association. The new information about behaviour of rock-dwelling cichlids in their natural environment would not have become available without the support of the companies SCUBAPRO (Germany) and SEAWAY (Germany). The efforts and enthusiasm of Ludwig Schadhauser (journal "Wild about Animals") was instrumental in securing much of the financial support. Last not least I want to thank the publisher Dirk Verduijn for his pleasant co-operation in the production of this book.

I use in this book "we" and "I" at different places. When it concerns general observations, discoveries of "new" species etc., I use "we". When conclusions are drawn from our results, and decisions made that are mine, and do not necessarily reflect the opinion of all other team members, I use "I".

Lake Victoria: climate, limnology and history

Climate and limnology

Lake Victoria, the biggest tropical lake, and the third biggest lake on Earth, is situated on the East African plateau at 1134 m above sea level, between the Central African Rift in the West and the East African Rift in the East. It stretches across the equator, extending from 0.2° North to 3.0° South and is surrounded by three countries, Tanzania (49 % of lake surface, roughly 60% of shoreline), Uganda (45% of surface, roughly 30% of shoreline) and Kenya (6% of surface, roughly 10% of shoreline). The lake has a large catchment area (194,200 km²; Piper et al. 1986) with several bigger rivers draining into it. The largest one, the Kagera river in the West, drains the mountains of Rwanda and Burundi and hilly rainforest areas in western Tanzania. The second largest, the Nzoia river and several smaller ones in the Northeast, drain the forested mountains of western Kenya. The third big river, the Mara, also has its origin on these mountain slopes. However, it also drains, together with smaller and semipermanent rivers, the relatively dry Serengeti plains in the Southeast.

The lake is a huge sink with a single outlet, the river Nile, breaking out from the lake at its northernmost point and connecting Lake Victoria to Lake Kyoga, a shallow, extremely denticulated extension of the Nile. Downstream of Lake Kyoga, the waters of the Nile plunge down Murchison Falls, which are a formidable barrier to migration of fish. It is Murchison Falls that isolate the Victoria basin from the ichthyofauna of the rest of the Nile and its associated Lake Albert.

The climate is equatorial with two wet seasons, in the southern parts one between October and December, the other

Cichlids at the rock-sand interface at a depth of 6 metres at Makobe Island.

Figure 1. The catchment area of Lake Victoria (surrounded by stippled line), and adjacent catchment areas of (clockwise from top) Lakes Kyoga, Eyasi, Tanganyika/Kivu, Edward/George, and Albert. Arrows indicate the direction of water flow in the rivers. Lake Victoria is connected to Lakes Edward/George through the Katonga River. However, the area in which the river undergoes reversal of its flow direction is difficult to penetrate for cichlids. It is a papyrus swamp in which waters have very low oxygen concentrations.

one between February and April. Annual rainfall averages about 1000-1500 mm, the northwest being more humid than the southeast and east. Differences in rainfall are reflected in the natural vegetation surrounding the lake. Mighty rainforests grow along the northwestern shores and on the huge island archipelagos in the Ugandan part of the lake. Less luxurious evergreen forests are found at many places along the west and on islands in the southwest (e.g. Rubondo Island), south (e.g. Kome Island) and southeast (e.g. Ukerewe and Bwiru Islands). The mainland shore in the south is dominated by shrub vegetation and grassy hills, while very hilly areas in the southeast (e.g. Mwanza Gulf) with heavily eroded granite rocks are dominated by deciduous and semi-deciduous shrubs and euphorbias. The half-evergreen vegetation on many small rocky islands in the Southeast is dominated by fig trees and euphorbias. In the East the grassy Serengeti plains reach the lake shores. This part of the lake region receives the lowest rainfall.

The lake basin morphology of Victoria is very different from that of the rift lakes. It is basically saucer shaped, with a large open water body of between 60 and 100 m depth, a greatest length of 400 km and greatest width of 320 km. The comparatively little depth, combined with the wide surface, allowing annual total mixis of the water mass, makes it that until the recent changes took place, the entire water body was inhabitable for fish. Apart from the open waters and the wind and wave exposed western and eastern shore lines, the lake has relatively more sheltered shore lines along the large gulfs (Napoleon Gulf, Kavirondo Gulf, Speke Gulf, Mwanza Gulf, Emin Pascha Gulf) and within the island archipelagos in the north, southwest and southeast.

Due to the high altitude, temperatures stay moderate, with daily mean maxima of about 28°C and mean minima of about 16°C in Mwanza (based on data from the meteorological station Mwanza). Water temperatures are likewise moderate. We measured maxima of 27°C and minima of 21°C. Heavy SE winds during the dry season (June to September) stir up the lake and cause mixis of the water body. The water of Lake Victoria has a neutral to slightly alkaline pH. Fryer & Iles (1972) give a range from 7.1 to 9.0. We measured a similar range of pH (6.9 to 9.0), and a hardness of between 2 and 8°. The conductivity lies, according to Fryer & Iles (1972) between 98 and 145 mho./cm. The water transparency is low compared to that in Lakes Malawi and Tanganyika but not everywhere as low as frequently assumed. In the early days of this century, visibility reached up to 8 m (Graham 1929). Since then it has decreased considerably. The maximum measured by us at offshore stations during the 1990s was 4.2 m, however, at many places transparency is below 1 m.

Limnological studies have been carried out on Lake Victoria in the early years of this century by Graham (1929) and were taken up again much later (Talling 1957, 1966, Akiyama et al. 1977). Recently limnological work has been intensified, with data collecting, however, largely restricted to northern parts of the lake. This work shows that dramatic changes have been happening in the nutrient household of Lake Victoria. Concentrations of nitrogen are increasing since the 1920s, those of phosphate since the 1950s, induced through precipitation and human activity in the catchment area, such as agricultural and urban developments and deforestation (Hecky 1993, Gophen et al. 1995). Increasing phytoplankton densities and frequent algae blooms are the consequence (Ochumba & Kibaara 1989, Lehman & Branstrator 1993, Mugidde 1993). Indications that the lake is undergoing eutrophication have been recorded since the 1960s (Hecky 1993), and have become more apparent after the population upsurge of the introduced Nile perch, and the concomitant decline of the sublittoral haplochromines (Goldschmidt et al. 1993). Massive fish kills have been observed (Ochumba 1987) and the recent investigations discovered that most of the deep water in the formerly entirely oxygenated Lake Victoria, is now consistently anoxic (Hecky et al. 1994, Gophen et al. 1995). There are indications that annual vertical mixing of the water body does not reach the deep layers any more (Gophen et al. 1995). With these recent alterations the deeper waters of Lake Victoria become probably as hostile to fish life as are those in Lakes Malawi and Tanganyika. Upwelling of hypoxic water has been observed also at steeply sloping rock shores (N. Bouton pers. comm., pers. obs,), where it poses a threat to rock-dwelling cichlids.

The sources of the Nile at Jinja in Uganda.

Geological history of Lake Victoria

The African continent is an ancient land mass, that after a long period of relative tectonic stability, began to experience earth movements and volcanic activity in the Miocene and Pliocene epochs (roughly about 20 to 5 Myrs ago). In the course of these, the rifts formed and at several places started to fill up with water, as a consequence of river severance. The position of modern Lake Victoria was occupied by a highland ridge, constituting, near what is now the eastern shore of the lake, a watershed between rivers that flew westward via modern Zaire river system into the Atlantic ocean, and others that flew eastward to the Indian Ocean (Cooke 1958). Smaller lakes existed by that time and fish fossils from lacustrine deposits were found. The fossil ichthyofauna had little in common with the modern Victorian fauna. It contained *Oreochromis* of the *O. mossambicus*-type (today confined to rivers flowing into

Zinga Island was separated from the mainland (below) a few decades ago. If the water level rises further, the island will be split into two.

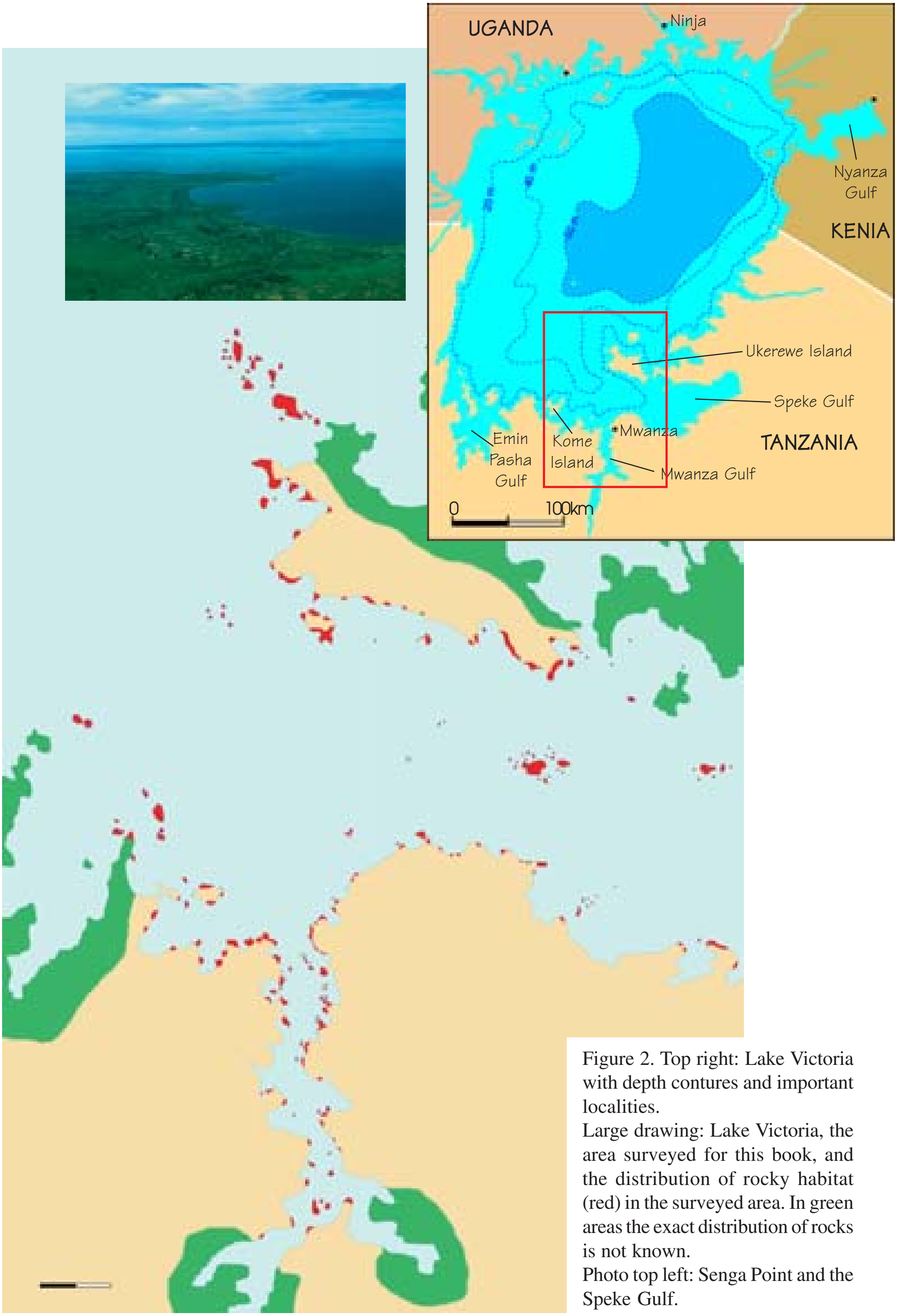


Figure 2. Top right: Lake Victoria with depth contures and important localities.
Large drawing: Lake Victoria, the area surveyed for this book, and the distribution of rocky habitat (red) in the surveyed area. In green areas the exact distribution of rocks is not known.
Photo top left: Senga Point and the Speke Gulf.

the Indian Ocean), other cichlids that could not be identified, *Polypterus* and *Lates* (Fryer & Iles 1972). Thus, it consisted mostly of fishes that do not naturally occur in modern Lake Victoria but are characteristic either for the East African, or for the nilotic fauna. The extinction of these taxa is considered evidence for complete drying-up of the lakes before modern Lake Victoria came into being. The latter process cannot yet be accurately dated but there are indications that the region west of the modern lake got elevated about 500 000 years ago through warping. As a result, the westward flowing rivers (proto-Nzoia/Katonga and proto-Mara/Kagera) were ponded back, and an internal drainage system was formed. The former river beds broadened, and riverine environments got transformed into lacustrine environments, edged by extensive swamps. Based on the topography of the present day drainage system, it has been suggested that at least three such lakes have existed (Fryer & Iles 1972). Relatively small local earth movements may have been sufficient to break and create watersheds among the lake-like river arms, and to cut off bays from the major body. It has been suggested that modern Lake Kyoga, a semi-lacustrine extension of the Victoria Nile, is representative for this riverine-lacustrine transitional state (Fryer & Iles 1972). It is neither known how long the transformation of the river system into a lacustrine environment took, nor how many isolated lakes were formed, and whether they stayed sufficiently long isolated to be of interest in the reconstruction of the evolutionary history of the Victorian cichlid flock. Nevertheless, cichlid researchers till today draw heavily on this transitional phase to explain speciation (see the chapter about the species flock). As the saucer was eventually filled, the water broke through the northern watershed, forming the Victoria Nile.

There is good evidence for that Lake Victoria's shoreline was instable ever since its formation. About 60 000 years ago the lake was much bigger, extending westwards into modern Kagera valley. Several satellite lakes and semi-lacustrine water bodies have remained there (e.g. Lakes Ihema, Twamwala and Rushwa). The maximum extension of the lake was followed by several phases of lake level recessions, which have been suggested to correlate with phases of increasingly deep incision of the Victoria Nile outlet. Not only tectonic activities, but also climatic fluctuations contributed considerably to the instability of the lake shore topography. During the last glacial period (about 20,000 years ago) temperatures in equatorial Africa were considerably lower than today. When the temperature rose (about 15,000 years ago), the ratio of precipitation to evaporation must have changed in favour of evaporation, which has sometimes been assumed to have caused a drop in lake level (Fryer & Iles 1972). This has largely been confirmed by recent micro-fossil (e.g. unicellular algae, sponge needles, tree pollen) analysis of sediment cores from Lake Victoria, that provided important new insights into the lake's recent history.

The micro-fossil record currently extends back to 25,000 years BP, and shows that the lake level has been fluctuating very much within this period (Stager et al. 1986). Maximum aridity occurred between 15,000 and 13,000 BP. Since the deepest sediment core has been taken at a water depth of 66 m, it cannot yet be said, whether Lake Victoria dried up completely, though the concomitant reductions in the levels of Lakes Tanganyika and Malawi would suggest so (Owen et al. 1990). However, it seems certain, that between 14,750 and 13,700 BP the water level fell below the level of the coring site. This is about 70 m deeper than now, and means that the lake was reduced to 20% of its present surface area, and that its circumference was reduced by more than 45%. Maximum depth was merely 26 m (see text figure 10 in the chapter on evolution). This is of major interest in the discussion about the evolution of Lake Victoria's species flock, and the rock-dwelling cichlids in particular. The south-eastern part of the lake, the rocky shores of which were surveyed by us as reported in this book, was entirely dry! The lake, however, did not separate into disjunct water bodies. After 13,700 BP the lake level rose and was 8,000 BP considerably higher than today. A second overflow may have existed south of present days Mwanza Gulf. Since then, the water level is recessing again (Stager et al. 1986). The most recent major recession has been dated to about 3700 years ago (Temple 1967), another date of interest in the discussion about the evolution of rock-dwelling cichlids. Interesting are also changes that happen on very short term: A comparison of the present shoreline topography (see photo 16) with a detailed map from 1908 (revised reproduced on page 65) shows, that the water level is currently about two metres higher than it was by 1908. Several rocky areas that were peninsulas by then are now separated from the mainland by shallow water (Ndurwa Point = Ndurwa Island, Kawangazi Point = Igombe Island, Zinga Point = Zinga Island).

Postscript:

Latest research results published in the journal *Science* of 23 August 1996 make most likely that Lake Victoria had entirely dried up 12,400 years before present (Johnson et al. 1996).

The cichlid species flock

The species flock of haplochromine cichlids in Lake Victoria has been considered the most striking example of explosive evolution and adaptive radiation among vertebrate animals (Wilson 1994). Its complex ecology and evolutionary history captivates the minds of biologists since more than a century ago. Though the picture of the flock, and of its causal and temporal context, has become refined over several generations of research, many basic questions are still unresolved. Among them the questions about the ancestry of the species flock, and why and how the species became that many (modes of speciation).

The question, whether the haplochromine cichlids of Lake Victoria form a species flock in the strict sense (*sensu* Greenwood 1984), that is, a monophyletic group, derived from one common ancestor, has long been debated. An ancestral species would likely be a riverine (river-dwelling) cichlid, similar to those haplochromines that inhabit the rivers of modern East Africa. Frequently it has been assumed that it may have been close to a group of riverine species, usually referred to as the *Astatotilapia bloyeti*-complex. Populations of this complex inhabit almost every East African river that drains to the Indian Ocean, but have not unambiguously been recorded from river systems connected to Lake Victoria. Molecular data confirm that *A. bloyeti* is closely related to the Victorian flock (Meyer 1993). However, since the rivers that were "back-ponded" to form Lake Victoria, drained to the West and not to the Indian Ocean, it seems likely that the closest relatives of the flock's ancestor are found in some of the smaller westward flowing rivers, that are now captured between the ridges of the eastern and central African rifts. More recent molecular work supports this (Meyer at al. 1994).

Although anatomical studies so far failed to produce any evidence for a monophyletic origin of the Lake Victoria cichlid species flock, the now available molecular evidence is positive (Meyer et al. 1990). Neverthe-

Astatotilapia bloyeti from a river flowing into the Indian Ocean.

less, because not only one, but several rivers were back-ponded to form Lake Victoria, it is well possible that more than one riverine population founded the flock. Whether the flock is of mono- or oligophyletic origin, strictly speaking, depends then on whether the founding populations had, before the lake was formed, been long enough isolated in their river basins, to behave as separate species on reunification, or whether they merged into one. However, I am not sure whether this would ever be resolved, and the difference does little to the amazing speed with which the founder population(s) evolved into an assemblage of hundreds of species that, as E.O. Wilson has put it, fill almost all major niches available to freshwater fishes as a whole (Wilson 1994).

Recent estimates of the age of the flock vary between 200,000 years (Sage et al. 1984, Meyer et al. 1990) and 14,000 years (Owen et al. 1991). Despite its very recent origin which is reflected in very little genetic differentiation (Sage et al. 1984, Meyer et al. 1990), the Victorian cichlid species flock is ecologically not less diverse than those of the older Lakes Malawi and Tanganyika. The modern haplochromine cichlids of Lake Victoria can be grouped into at least 16 different feeding groups, so called trophic groups (Greenwood 1974, Witte & van Oijen 1990), from small invertebrate and fish fry predators, similar to those living in today's rivers, to tiny plankton feeders, large fish hunters, snail eaters and algae scrapers. They inhabit every available lacustrine habitat from narrow crevices among rocks, water lily beds, and floating papyrus islands, to the entirely unsheltered pelagic zone of the open water body, and to the deepest parts of the

View on Anchor Island from Saa Nane Island.

lake that are not reached by daylight.

With the latest update presented here, more than 500 different species of haplochromine cichlids are known from Lake Victoria. The true species number is almost certainly even higher. Several writers that compared the ecological composition of the three large cichlid "flocks" (note: the Lake Tanganyika "flock" is not a species flock in the strict sense because it has been shown that it is polyphyletic (Sturmbauer & Meyer 1993)) noted two apparent peculiarities of the Lake Victoria flock: a very high proportion of piscivorous cichlid species (Fryer & Iles 1972, van Oijen 1982, Greenwood 1984) and a very low proportion of rock-dwelling algae scrapers and other rock-restricted cichlids (Fryer & Iles 1972, Greenwood 1984, Ribbink 1991, Goldschmidt & Witte 1992). This picture of the overall ecological shape of the flock is changing considerably with the discovery of the rock-dwelling cichlid assemblage described in this book, and is becoming more similar to that of the "flocks" in the other lakes (Seehausen 1996a). It is likely that the resemblance will become more evident, as more of the littoral habitats along the lake shore will get surveyed. However, a high proportion of piscivorous cichlid species may remain a peculiarity of the original Victorian flock.

The term adaptive radiation stands for ecological diversification of a founder stock (the ancestral species), going hand in hand with splitting of its gene pool into a multitude of isolated gene pools (species), each of which occupies only a small part of the total ecological space. Adapted to the different niches, these species can utilize the particular resources of any niche more efficiently than the non-specialized ancestor could, but are less efficient in utilizing other niches which have their own specialists. Consequently each species is rather narrowly restricted to its niche. This concept appears simple and is often regarded an obvious fact, particularly in aquarium literature about cichlid evolution. However, reality seems much more complicated. For characters which common sense considers adaptive (e.g. many rows of densely set teeth in the mouth of an algae scraper), actual adaptiveness (= possession of the character gives competitive advantage over individuals that do not possess it) has rarely been demonstrated. This gap in the argument of adaptive radiation has sometimes been hotly debated (see for instance Liem 1980 and Barel 1983). Some indirect evidence for the adaptivity of interspecific differences in the morphology of the feeding apparatus in Lake Victoria rock cichlids has recently been produced (Seehausen et al. in press [a]). Much work remains to be done to understand the phenomenon of adaptive radiation. It is often assumed that competition between species is driving adaptive radiation, but again, well demonstrated evidence for interspecific competition in cichlid assemblages is very rare, and nothing is known about its evolutionary significance.

The term adaptive radiation is mostly used to describe the enormous diversification of the feeding apparatus and feeding behaviour in cichlids (Fryer & Iles 1972, Greenwood 1974, 1981). Lacustrine cichlids, however, radiated in a number of different, though not independent traits, such as substrate affinities and depth distribution. This aspect of adaptive radiation was long overlooked by scientists and aquarists working with Victorian cichlids alike. An apparent eurytopy of Lake Victoria cichlids, as expressed by generally weakly developed habitat specificity (Fryer & Iles 1972), and absence of geographically restricted distributions within the lake (Fryer & Iles 1972, Greenwood 1974), was, and by some people still is considered a striking difference between Victorian and Malawian/Tanganyikan cichlids. Evidence against these assumptions has been brought forward by several authors (Witte 1984, Goldschmidt et al. 1990, van Oijen 1991, Seehausen & Bouton 1996a, in press) and much new evidence for habitat specificity and intralacustrine endemism is provided in this book. Less dramatic, but nevertheless existent among Victorian cichlids, are radiations in social behaviour and in reproductive strategies (table 2, Goldschmidt & Goudswaard 1989), for which adaptiveness could be assumed as well. A dramatic radiation has finally occurred in male coloration, adaptiveness of which is not quite apparent on the first glance.

The chief theoretical puzzle created by species flocks is the process by which they grow (Wilson 1994: 102). Neither the mechanisms of growth (i.e. speciation) nor the mechanisms by which growth is controlled (how many species can coexist) are yet fully understood by biologists. Several potential ways of speciation in cichlid lakes have been suggested. Reduced to the essential message, these are, (1) classical allopatric speciation by geographical isolation, (2) micro-allopatric intralacustrine speciation by ecological isolation, (3) sympatric speciation.

The evolutionary significance of speciation in sympatry, in the absence of geographical and ecological barriers that prevent interbreeding among diverging forms, has long been disputed. Recently, however, strong supportive evidence for its role in cichlid species flock formation is accumulating from both empirical (e.g. Schliewen et al. 1994), and theoretical work (e.g. Turner et al. 1995). The potential role of sympatric speciation should no longer be neglected in attempts to explain evolution in Lake Victoria.

As a logical consequence of the assumption that Victorian cichlids display little habitat specificity, micro-allopatric speciation has not been considered much either in the attempts to explain the explosive evolution of Lake Victoria cichlids (but see Ribbink 1991). Instead the focus has long been on allopatric speciation in isolated lake basins. This idea was predominantly entertained by P.H. Greenwood who used Lake Nabugabo as a striking example of rapid speciation in geographical isolation. This former lagoon is cut off from the main lake since no more than 4000 years ago, but is inhabited by 5 endemic cichlid species. Ongoing work on other satellite lakes shows that Nabugabo is certainly no exceptional case (L. Kaufman pers. comm., Seehausen et al. in press [b]). Kaufman and Ochumba (1993) phrased the term "species pump" for the process by which new species are added to the flock of Lake Victoria when periods of high water level alternate with such of low water level and speciation in lake side lagoons. However, species endemic to satellite lakes, usually differ from their nearest relatives in Lake Victoria predominantly in coloration and not much is known yet about whether these differences would be sufficient to prevent interbreeding when the geographically isolated siblings would be reunited by a rise of water level. Thus, the speed with which differences between satellite populations and the main lake populations evolve, support the hypothesis of speciation in separated lake basins, but do not prove it.

For several reasons speciation by geographical isolation in isolated lake basins is most unlikely to be the only mechanism that accounts for the species flock formation in Lake Victoria.

(1) it is difficult to perceive how repeated fragmentation and re-unification of the lake could have led to the evolution of more than 500 species.

(2) splitting of gene pools in geographical isolation cannot explain the radiation into various feeding and habitat niches. The pattern of major niche complementarity is better explained by intralacustrine diversification of the kind recently demonstrated for several fish groups in geologically young post-glacial lakes of the northern hemisphere (Bentzen & McPhail 1984, Bentzen et al. 1984, Skúlason et al. 1989, Taylor & Bentzen 1993, and references herein).

(3) satellite lakes usually have only a few habitat types, they are mostly shallow, surrounded by swamps, have reed and papyrus edges, muddy bottoms, some shallow open water and maybe some sand bottom. It is highly unlikely that rock-restricted cichlids, deep water-restricted cichlids or pelagic open water dwellers could ever have evolved under such conditions. Lineages with specific habitat demands such as pelagic *Yssichromis* and rock-dwelling

Neochromis are absent from the small present-day satellite lakes, and poorly represented in the biggest satellite lakes.

(4) the strongest argument for speciation modes other than classical allopatric, is the high degree to which regional endemism is developed among the rock-restricted cichlids, that cannot be correlated with possible distribution of former satellite lakes (see the chapter on evolution).

It seems therefore certain that modes of speciation, other than classical allopatric, are involved in the formation of the Lake Victoria cichlid species flock.

As much as the cichlid flock of Lake Victoria is an example of explosive speciation, it is one also of mass extinction. Nile perch, *Lates* spec., which since its extinction about 10 to 20 Myrs ago (long before the cichlid flock came into being), was absent from the Victoria drainage, was brought into the system by man in the 1950s. It had been kept in aquaculture in Uganda for some years, and an introduction into the lake was discussed and disputed, when in the late 1950s some individuals somehow got into the lake. How this happened is not quite clear, however, subsequently the lake was stocked several times deliberately in the early 1960s with Nile perch from at least two sources, Lake Albert and Lake Turkana (Harrison 1991). During the first 25 years after its introduction, Nile perch did not exert any apparent impact on the cichlid fauna. Nile perch catches were low, until, in the early 1980s, they increased explosively. Simultaneously, many other fish species declined, and most dramatically the haplochromine cichlids. Already in the second half of the 1980s Nile perch comprised more than 90% of the total catch weight of trawlers, and cichlids had basically disappeared from the catches (Oguto-Ohwayo 1990, Barel et al. 1991). Within five to ten years between 150 and 200 endemic haplochromine species disappeared, many of which probably became extinct (Witte et al. 1992).

Since Nile perch does not inhabit all habitats alike, and does not forage on all kind of cichlids alike (Witte et al. 1992), the predator reshaped the species flock dramatically but is unlikely to cause the destruction of the entire flock (Seehausen 1996a). It is the species with largest habitat overlap with Nile perch, and the larger species, in particular the fish eating cichlids, that were exterminated almost entirely. Some small detritus and zooplankton feeders apparently manage to coexist with Nile perch (Witte et al. 1995) and larger species diversity currently survives in a number of refugia (Kaufman & Ochumba 1993, Seehausen & Witte 1995). These are habitats, not well accessible to Nile perch, or in which its hunting efficiency is reduced. The most species rich of these refugia are rocky shores, islands, and small, isolated rocky reefs (Seehausen et al. in press [b]). The predator-reshaped cichlid species flock of Lake Victoria is in its ecological composition rather similar to that of Lake Tanganyika, a flock that evolved in the presence of Nile perch. Rocky habitats may play a particularly important role in the further evolution of Victorian haplochromines.

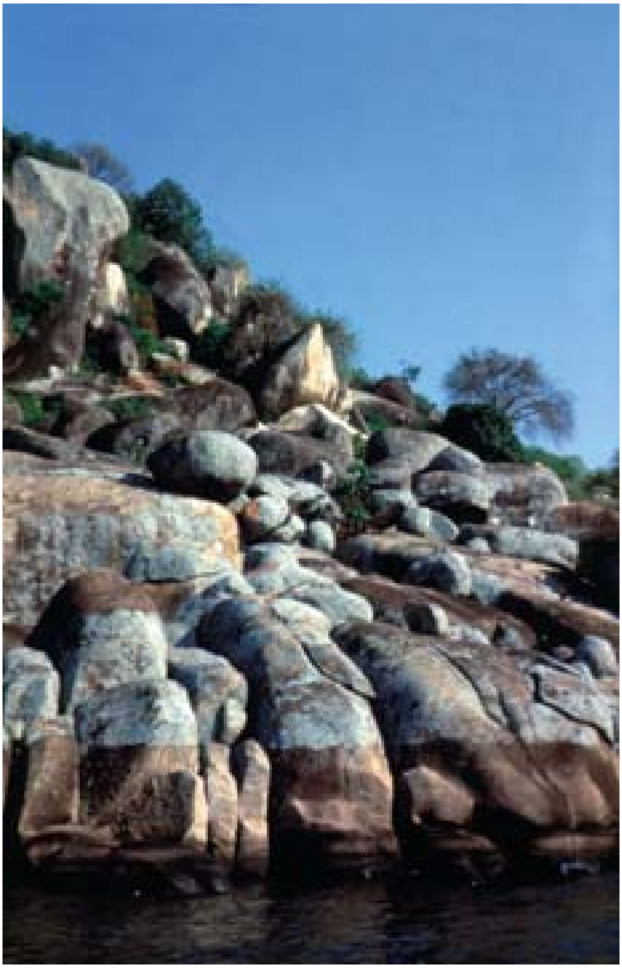
Postscript:

While this book went into press, work was published by Johnson et al. (1996) that makes most likely that Lake Victoria had entirely dried up as recently as 12,400 years ago. The authors studied lake bottom sediments by seismic reflection profiles and piston cores. They found a terrestrial soil (vertisol) horizon with grass roots in the deepest part of the lake under an only 7 m thick layer of lacustrine deposits that had sedimented since the area is flooded again. According to the authors, during the dry period the lake was neither split into several basins, nor would the climate have allowed the persistence of satellite lakes. The authors conclude that most of the endemic cichlid species of the lake have evolved during the past 12,400 years. Species formation in Lake Victoria must have been largely intralacustrine, and was more explosive than most evolutionary biologists ever imagined.

The *Mbipi*, overlooked subflocks like the Mbuna of Lake Malawi?

Among more than 100 haplochromine cichlid species, that Greenwood described and redescribed from Lake Victoria, was one strictly lithophilic (rock-restricted) algae scraper, which later, in Greenwood's (1980) generic revision became the sole Victorian representative of the genus *Neochromis*. Greenwood seemed convinced that strictly lithophilic cichlids were uncommon in Lake Victoria, and was surprised when the Haplochromis Ecology Survey Team discovered a group of such fishes 30 years after he had started working on the lake (van Oijen et al. 1981, Greenwood 1994). This group consisted of eleven species (Witte et al. 1992), one of which has in the meantime been described (Witte-Maas & Witte 1985). It took another decade until about 10 further rock-restricted species were discovered between 1986 and 1991, when J. Sevenster, N. Bouton, Y. Fermon and I visited some rocky islands that had not been sampled previously. Based on these results, it was predicted that the number of rock-dwelling cichlids in the lake is likely to be even much higher (Seehausen 1992). Irrespective of this, it was a great surprise again to ichthyologists, who had been working on Lake Victoria before, when the survey of rocky shores in southeastern Lake Victoria that we conducted between 1991 and 1296, produced about 90 more, previously unknown species of strictly lithophilic cichlids. It is just now becoming apparent that a large and taxonomically diverse part of the Victorian cichlid species flock had simply been overlooked in the past. This newly discovered assemblage of rock cichlids in many respects closely resembles the *Mbuna*, the rock-dwelling cichlids of Lake Malawi (Nyasa), and is for cichlid hobbyists certainly no less an attraction, and one of the most interesting components of the Victorian flock.

The majority of the rock-restricted cichlids of Lake Malawi were considered, by fishermen, taxonomists and aquarists, a group on its own within the Lake Malawi



Steep rocky coast are rare along the Victorian shoreline.

cichlid species flock long before molecular biologists largely confirmed their status as a subflock — i.e. a group of species derived from one common ancestor within the larger flock. The Tumbuku term *Mbuna* with which fishermen at Lake Malawi collectively denote the either dark or brightly coloured rock cichlids, was adopted by biologists and aquarists. Similarly do fishermen at southern Lake Victoria have a collective name for Victorian rock cichlids: *Mbipi*. In the Kisukuma language, which is the most commonly spoken language among fishermen in the southwestern lake region, *Mbipi* means as much as "the dark ones".

Fishermen were aware of the existence of the *Mbipi* long before biologists happened to "discover" them. Fishermen are frequently rather good naturalists and parallels between their popular classifications of fishes, and the scientific classifications made by biologists, are common. With names like *Mbuna* and *Utaka*, fishermen of Lake Malawi defined groups among the cichlid species, that are very similar to those, defined and delimited by biologists. The cichlids of Lake Victoria are divided by fishermen into three major groups, *Furu* (*Haplochromis*), *Komaga* (*Astatoreochromis*) and *Sato* (*Oreochromis*). Within the *Furu* three subgroups are commonly made: (1) *Mgobe-gobe*, the large-mouthed piscivorous species of the *Harpagochromis* and *Prognathochromis* lineages; (2) *Mbipi*, the rock restricted, mostly dark or brightly coloured cichlids; (3) all others. With the distinction of *Oreochromis*, *Astatoreochromis* and *Haplochromis*, the folk taxonomy identifies the same major groups of cichlid species in Lake Victoria that can be readily identified by molecular biology as the major cichlid lineages in Lake Victoria. With the recognition of piscivores and rock restricted haplochromines as subgroups within the *Furu*, the fishermen may prove to be ahead of biologists. Particular vernacular names for weed bed- or sand-dwelling cichlids do apparently not exist or are not much in use. Indeed the majority of the rock-restricted Victoria cichlids, more than those of other habitats, share a common facies that is recognized by the biologists working with them. Though difficult to quantify, it may indicate that they form a mono- or oligophyletic group within the Victorian flock.

On the basis of melanin pattern, two distinct groups within the rock cichlids can be discerned. The "Vertical bar *Mbipi*" are characterized by a number of simple vertical bars on the flanks which can be crossed by a faint mid lateral band, as exemplified by *H. (Neochromis) nigricans* and *H. (?) nyererei*. (photos on page 28; for explanation of the "(?)" see page 35). The "Chessboard *Mbipi*" are characterized by a mid and a dorsal lateral band crossing the vertical bars, reminiscent of the black and white pattern on a chessboard, as exemplified by *H. (Paralabidochromis) chilotes*. The melanin pattern is most easily seen in juveniles and females. Males, and less frequently females of chessboard species, when sexually active, may lose the longitudinal bands while retaining vertical bars. Though trophic (= feeding related) diversity is lower among "Chessboard *Mbipi*" than among "Vertical bar *Mbipi*", I did not observe any obvious correlation between melanin pattern and behaviour or habitat. In both groups exist more and less aggressive species, inhabitants of the rock surface, and those inhabiting crevices and caves, as well as different feeding strategists (compare also text figure 10a), though a group of planktivores has apparently evolved only among the "Vertical bar *Mbipi*".

The melanin patterns may therefore bear more relevance for the reconstruction of phylogeny (= line of descent), than anatomical characters that are often directly associated with ecology (see also Eccles & Trewavas 1989 for Lake Malawi haplochromines). My hypothesis is that the two melanin pattern groups represent two phylogenetically distinct lineages within the rock-dwelling cichlids of Lake Victoria. Apart from melanin pattern, the shape of the dentary (tooth carrying lower jaw bone) differs between the two groups. In the "Vertical bar

Mipi" the tooth carrying surface of the dentary runs slightly concave, and the outer teeth are implanted more or less upright (text figure 4). In species of the "Chessboard *Mbipi*", the tooth carrying surface of the dentary describes anteriorly a ventral inflection. In lateral view it runs somewhat convex. Consequently the anterior outer teeth are implanted slightly to strongly procumbently (text figure 4). Within each melanin pattern group, a number of species complexes can readily be recognized, based on anatomy. The anatomical diversity within each complex is only partly reflective of interspecific differences in ecology, and I am moderately confident that the majority of the species in each complex represent a monophyletic group. In the following account of the rock-dwelling cichlids, I present the species in these complexes. About 60 species are currently known in the "Vertical bar" group, slightly more than 20 in the "Chessboard" group.

Apart from the *Mbipi*, we found among rock-dwelling Lake Victoria cichlids several of the lineages described and defined by Greenwood (1980): *Psammochromis*, *Ptyochromis*, *Labrochromis*, *Lipochromis*, *Harpagochromis*, *Haplochromis*, lacustrine "*Astatotilapia*" and fluviatile *Astatotilapia*. All of these non-rock restricted lineages, except fluviatile *Astatotilapia*, have produced a few strictly lithophilic species, but none of them comes even close, in terms of speciosity at rocky shores, to the "Vertical bar" and "Chessboard *Mbipi*". If my phylogenetic hypothesis is correct, the rocky habitats of Lake Victoria are dominated by two phylogenetic superlineages, which both have undergone considerable secondary radiations. These radiations are particularly apparent in the Vertical bar superlineage. It contains large groups of algae scrapers, insect eaters, and plankton eaters, and thus, has radiated to tap the three major food sources found in rocky habitats. It is not impossible that certain anatomical and ecological specialists among the rock-cichlids, that I currently assign to other lineages on basis of their anatomy (e.g. *Lipochromis*), are trophically aberrant members of the vertical bar *Mbipi*.

Based on the similarity of melanin patterns and on jaw and dental morphology, a close relationship between the "Vertical bar *Mbipi*" and the *Haplochromis* lineage *(sensu stricto)* on the one hand, and between the "Chessboard *Mbipi*" and the *Psammochromis* lineage on the other hand seem likely. The first of these assumed relationships would be congruent with Greenwood's (1980) hypothesis of a superlineage consisting of *Neochromis*, *Xystichromis* and *Haplochromis*. It may have to be extended to include all species complexes of "Vertical bar *Mbipi*". Similarly the assumed relationship between *Paralabidochromis* and *Psammochromis* would be congruent with Greenwood's hypothesis of a *Psammochromis*-*Macropleurodus* superlineage, which contains *Paralabidochromis*. This superlineage does not only overlap in species composition with the "Chessboard *Mbipi*" but shares anatomical characters with both *Mbipi* superlineages. These are in particular aspects of the general head anatomy: a relatively short lower jaw, supported by muscles that allow powerful biting, and the tendency to increase the number of inner tooth rows. These characters appear to be adaptations to feeding upon benthic organisms, that need to be removed from a firm substrate by biting, and may well be independently derived. In that case they would not indicate a recent shared ancestry of the *Psammochromis-Macropleurodus* lineage, including the "Chessboard *Mbipi*", with the "Vertical bar *Mbipi*". However, it is equally well possible that an ancestral species, after having achieved the ability for forceful biting, invaded all feeding niches that demand for it, and consequently split up into lineages with different feeding ecology. In that case the *Psammochromis-Macropleurodus* superlineage could perceivably be the sister taxon to the "Vertical bar *Mbipi*". I hope that developments in molecular genetics and other phylogenetic techniques will soon make such hypotheses testable.

Among the now over 130 species of

rock-restricted and other rock-dwelling cichlids, we found high degrees of regional endemism and distinct zoogeographical patterns in distribution. Because to date we have surveyed merely about 15% of the rocky shores of Lake Victoria, I expect many (probably over 200) more rock cichlid species to await scientific discovery. That their extreme diversity was simply overlooked during several decades of field research, is perhaps due to the murky waters of Lake Victoria that make faunistic and ecological work much more difficult than it is in the clear waters of Lakes Malawi and Tanganyika, but not less fascinating.

H. nyererei from Ruti Island; an F_1 male showing a typical vertical bar pattern.

A male *H.* "rockkribensis" in the aquarium, exhibiting a typical chessboard pattern.

Taxonomy of rock-dwelling cichlids

Species recognition

Because stenotopic rock-dwelling cichlids form many small isolated populations, species recognition and delimitation among them is more difficult than among cichlids of the sublittoral and open waters. In the *biological species concept* (defined by Mayr 1942) a species is a population or group of populations whose members have the potential to interbreed with one another in nature, producing fertile offspring. A species is isolated by intrinsic ecological, behavioural or other barriers from other species with which it does not successfully interbreed in nature. This concept cannot be strictly applied to rock-dwelling haplochromines. Because populations, living at different islands (or habitat islands), are effectively isolated from each other by stretches of sand bottom and open water, it is often impossible to judge whether members of two *would* interbreed if they could meet. We found that some anatomical and/or coloration differences exist among any two island populations in most of our research area, and it has been shown that gene flow is restricted even among those that are topographically not far from away each other (Dorit 1990). Thus, one could with some justification declare most populations different species. This is not only likely to be wrong in most cases, but would veil morphological and ecological diversity by giving the same taxonomical rank to uncountable very similar forms (indeed thousands) and much fewer more different forms. Such a system would furthermore not provide any information about phylogenetic relationships among populations. Such information, however, is required to understand evolution of rock-dwelling cichlids, and to interpret ecological patterns in an evolutionary context. The task of the taxonomist must therefore be to identify groups among populations that are closer related to each other than to others, and to define and delimit species among them.

Ribbink et al. (1983), when confronted with the same problem in Lake Malawi (Nyasa), decided to apply the *Specific Mate Recognition System* (SMRS) described by Paterson (1978) to define and delimit species. This system stresses the importance of mutual recognition among individuals of a species as partners in reproduction. Sympatric forms that do not recognize each other, and thus do not regularly interbreed, are considered different species, no matter how similar they are to the human eye. In a number of field studies of sympatric forms of Lake Malawi *Mbuna*, that were considered colour morphs of one species, it has been shown, that individuals of certain colour morphs that differ also in behaviour and microhabitat, do not mate with each other, and represent different species (Holzberg 1978, Marsh et al. 1981). Other studies had demonstrated earlier, that coloration and behaviour play important roles in cichlid communication during reproduction (e.g. Baerends & Baerends-van Roon 1950).

To categorize allopatric populations of *Mbuna*, Ribbink et al. (1983) assumed that if the characters, known to be important in species recognition (body shape, coloration, melanin pattern, behaviour, microhabitat), are the same among two geographically isolated populations, individuals would recognize each other if they would chance to meet. Individuals of other populations, however, that differ in one or more of these characters, so they assumed, would not recognize each other. Applying this concept strictly on some groups of *Mbuna*, Ribbink et al. emphasized differences rather than similarities, and considered populations, that differed distinctly in one of above

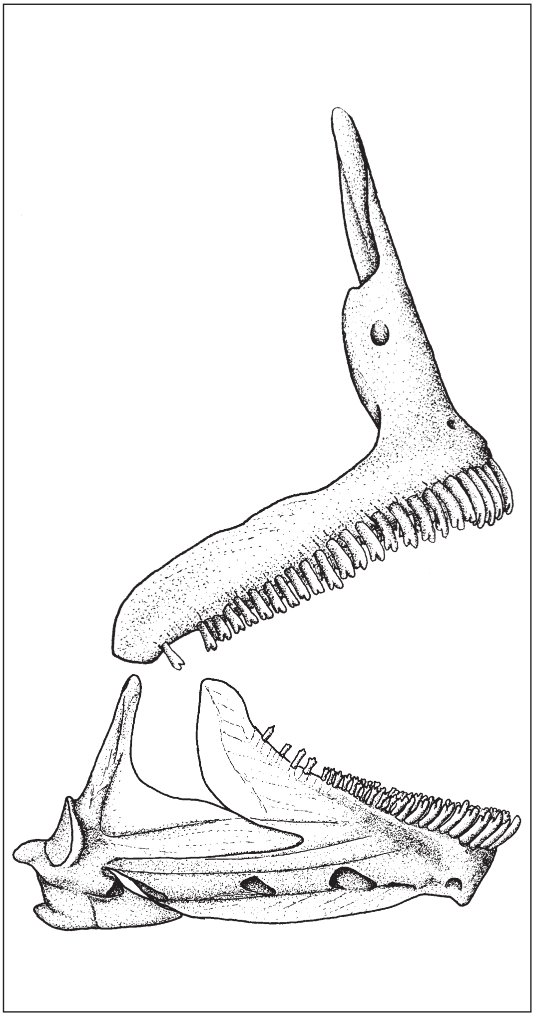


Figure 3: Jaws of a typical "Vertical bar *Mbipi*": *H. (Neochromis)* "velvet black". The outer teeth in both jaws are implanted more or less upright. Drawings made by R.J.C. Hoogerhoud from material of F. Witte and E.L.M. Witte-Maas.

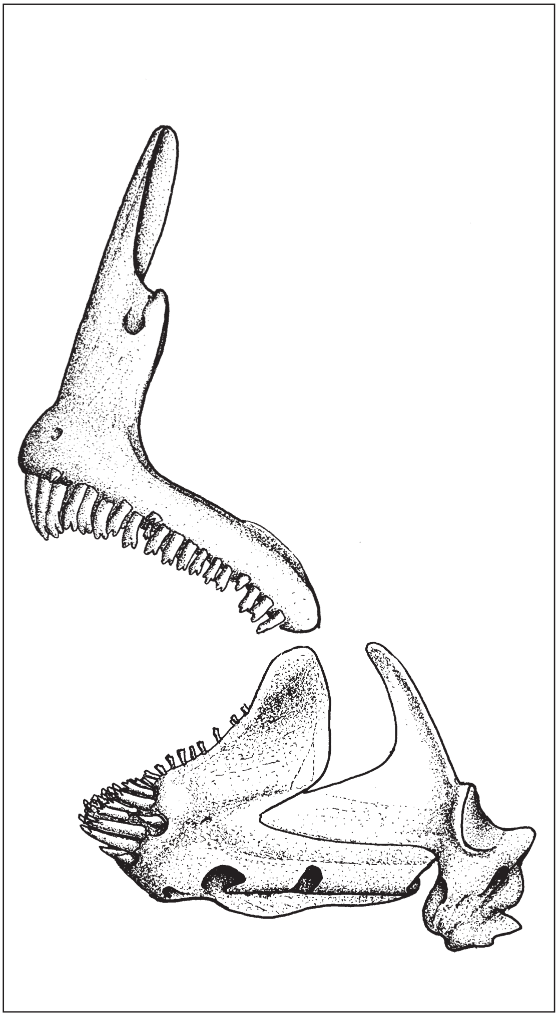


Figure 4: Jaws of a typical "Chess-board *Mbipi*": *H. (Paralabidochromis)* "rockpicker". The outer teeth in the lower jaw are implanted procumbently. Drawings made by R.J.C. Hoogerhoud from material of F. Witte and E.L.M. Witte-Maas.

mentioned characters, as being potentially non-interbreeding, i.e. different species.

For Lake Victoria cichlids, assortative mate choice among anatomically similar, but in coloration different forms of one species complex, has only very recently been shown in laboratory experiments (Seehausen 1996). While the results of that study support the applicability of the SMRS concept also to Lake Victoria *Mbipi*, there are also a number of problems involved with its application.

(1) The result of species delimitation among allopatric populations can depend on the geographical scale of the study. If between two populations only minor differences exist, and non of the SMRS characters is fundamentally changed, they will be considered conspecific. This is commonly the case among populations from nearby patches of rocky habitat. On the other hand, two allopatric populations that differ in anatomy and microhabitat distribution from each other as much as each of them differs from other sympatric species, would be considered two different species. However, they can turn out to represent merely extreme end points of a cline of gradual change, once the populations are known that live at localities lying topographically between those of the extreme populations. Such a case is known from *H. (Neochromis)* "velvet black". Western Speke Gulf populations, living in clear waters, are anatomically highly specialized epilithic algae scrapers of *Neochromis* type, that live predominantly on the rock surface. Those of the Mwanza Gulf and eastern Speke Gulf, living in less clear waters, are much less specialized as algae scrapers. They have less closely set teeth, fewer tooth rows, and a less steep dorsal head profile. At the same time they live more cryptically among rocks. If only the extreme populations would be known, they would probably be considered specifically distinct, though the two forms are connected by intermediate populations. Consequently, geographical and ecological patterns of distribution have to be considered in species delimitation.

(2) Different from studies on sublittoral- and open water-dwelling Lake Victoria cichlids, our studies on rock-dwelling species revealed a good number of cases of male colour polymorphism (Seehausen & Bouton 1996b). Thus, different male coloration alone is not sufficient evidence for two forms to represent different species. If, however, differences in coloration coincide with differences in ecology, as may be manifest in details of dentition or microhabitat distribution, the probability is much bigger that the two forms are reproductively isolated, or would be so if they chanced to meet. Nevertheless, final confirmation can only be obtained by studying mating behaviour.

As a consequence of these difficulties, I consider differences in one of the SMRS characters not as sufficient to separate species within complexes of closely related allopatric populations. I suggest to regard two forms of rock-dwelling cichlids as different species only if they differ in male coloration plus at least one other character. Furthermore I refer to distribution patterns wherever the available data allow. Thus, I consider two distinct forms that are connected by a cline of intermediate populations, as belonging to the same species, unless the extreme forms coexist sympatrically in parts of their range. In the latter case, we are dealing with chain species (see also the chapter on evolution). In such, and other cases, occasional gene flow may exist between two species, as long as both phenotypes remain distinct.

Generic taxonomy of Lake Victoria haplochromines

Haplochromis is probably one of the most broadly applied, and most inconsistently used cichlid generic names in popular and scientific literature. The genus *Haplochromis* was first described by Hilgendorf (1888), as a subgenus of the marine genus *Chromis* (damselfishes), for a Lake Victoria cichlid with a peculiar dentition (*H. obliquidens*, see page 230). In the course of the 20th century *Haplochromis*, given generic rank by Boulenger (1906), grew rapidly with the discovery of many "new" species from the Lake Victoria basin and Lake Malawi (Nyasa). In the late 1970s it contained more than 300 described and valid species, and was the most speciose taxon within the family Cichlidae. With the growing species numbers, also the generic limits grew far beyond the original diagnosis of Hilgendorf, and accommodated species with various tooth shapes. By that time *Haplochromis* contained many Malawian, and all but four of the endemic Victorian haplochromines. Those four represented four monotypic genera, differing from the other Victorian haplochromines in dentition characters, but obviously being closely related to them (Regan 1922).

The outer teeth of *H.* "velvet black".

Considering this classification unsatisfactory, particularly from a viewpoint of understanding the evolutionary history and phylogeny of this species rich assemblage, Greenwood (1979) split up the genus *Haplochromis*. Attempting to arrange the species in monophyletic groups (groups consisting of species derived from one common ancestor that is not shared with other groups) as genera, he tried to identify derived characters, shared by some species and not by others, which would indicate common ancestry to those that share them. In this way he divided the former *Haplochromis* species of the Lake Victoria basin over 16 new and resurrected genera and one of the monotypic genera that had already been nominal before. A similar revision was later done also for the Lake Malawi haplochromines by Eccles & Trewavas (1989). *Haplochromis* became restricted to species with a dentition resembling that described by Hilgendorf (1888).

The outer teeth of *H.* "blue scraper".

By the time of Greenwood's revision, slightly above 100 haplochromine species were known from Lake Victoria. In the years after the revision many "new" species were discovered, predominantly by the Haplochromis Ecology Survey Team (HEST), and researchers were confronted with difficulty when attempting to use the new genera. The problems were mainly the following: (1) New species could not be assigned to Greenwood's genera without extending generic limits (Snoeks 1988, as an example from Lake Kivu). (2) New species were found that bridged anatomical gaps between several genera *(Labrochromis* and *Gaurochromis*, Hoogerhoud 1984; *Yssichromis* and "*Astatotilapia*", Witte & Witte-Maas 1987; *Prognathochromis* and *Harpagochromis*, van Oijen 1991). (3) New data and a re-evaluation of Greenwood's data showed considerable overlap in supposedly diagnostic characters among species that Greenwood had assigned to different genera (Hoogerhoud 1984, van Oijen 1991).

Consequently these researchers opted to use the broad definition of the genus *Haplochromis*, that was in use prior to Greenwood's revision, rather than the new classification. Recently van Oijen proposed to exclude only the riverine *Astatotilapia* and to restrict *Haplochromis* to cichlids of the Lake Victoria basin, including the monotypic genera (van Oijen 1995).

When Hoogerhoud attempted to test Greenwood's delimitation of the genera *Gaurochromis* and *Labrochromis*, he took relative measurements of the oral and pharyngeal jaws, that should be different among the genera according to Greenwood. He demonstrated considerable overlap among the genera, found one species bridging them, and concluded that intraspecific variability is as great as the intergeneric differences, and the classification of the species into two genera artificial and arbitrary.

In a similar study, van Oijen (1991) analysed four quantitative characters of the skull (neurocranium; see for details Greenwood 1980, van Oijen 1991) that, according to Greenwood, are important for separating the two fish eating genera *Prognathochromis* and *Harpagochromis.* He re-measured the very 66 skulls of 43 piscivorous species upon which Greenwood had based his decision to split the piscivores into the two genera. In each of the characters he found greater overlap between the genera than Greenwood had found and concluded that the characters seem to form continuous morphoclines in which any division would be arbitrary. Thus, he considered a splitting of the piscivores into two genera not desirable.

Among the many new rock-dwelling cichlids, one encounters some similarly problematic species, but the majority can quite unambiguously be assigned to Greenwood's genera and some new lineages that were not yet known by the time of the revision. That generic limits have to be extended after discovery of new species, is not unusual in a fauna that is still poorly investigated. My experience with the classification proposed by Greenwood, is more positive than not, and I would like to call a few points into consideration, that may partly explain the negative experiences, other researchers had with it. Hoogerhoud and van Oijen based their rejection of Greenwood's generic division on intergeneric overlap in individual quantitative morphometric characters because these were (part of) the characters Greenwood used to delimit the genera. However, in clades (groups of related species) that underwent rapid speciation and adaptive radiation in an unstable environment, it seems to me unlikely that individual morphometric characters can ever accurately reflect phylogeny. Too large is the susceptibility of any one such character to the impact of temporal and spatial instabilities in the environment, to which it was exposed in the course of evolution. Because the susceptibility to any factor in the environment differs between characters, the combination of several characters is likely to be a better indicator of phylogeny than individual characters, since the impact of small scale adaptations is buffered against. Combinations of characters make up the "facies" of species that taxonomists perceive, and according to which they, sometimes rather subjectively, group them. It is often difficult to translate these "general appearances" into objectively quantifiable characters. However, multivariate statistics such as cluster analysis may be very helpful to objectively quantify combinations of several characters.

Though Hoogerhoud (1984) stated that the overlap that he found among *Gaurochromis* and *Labrochromis* could probably be reduced by using multivariate statistics, he did not discuss this further. I performed a cluster analysis (UPGMA) of his morphometric measurements of three nominal *Gaurochromis* and four nominal *Labrochromis* species. The result were two distinct species groups. One contained three *Labrochromis*, the other one three *Gaurochromis* plus one *Labrochromis* that was considered as bridging the genera by Hoogerhoud. Thus, though one species may have to be reassigned between them, Greenwood's distinction of the two genera is defendable on the measured characters, if they are combined. I performed the same type of cluster analysis also with the neurocranial measurements of van Oijen (1991) and again obtained two major groups which are quite similar to Greenwood's genera in their species compositions. Seventy one per cent of the *Harpagochromis* species clustered into one group, 91% of the *Prognathochromis* species into the other one. Thus, though again some species may have to be reassigned between them, the existence of two major lineages among the piscivorous Lake Victoria haplochromines seems defendable on skull anatomy when the combination of characters is quantified. *Psammochromis acidens,* a species that Greenwood assigned to another lineage despite overlap with *Harpagochromis* and *Prognathochromis* in individual characters, came out as the sister group to *Harpargochromis* and the two together as the sister group to *Prognathochromis*. One nominal species of *Prognathochromis* (*P. arcanus*) came out as the sister group of all the others, and should probably be removed from that genus.

Thus, in both cases multivariate analysis of critical characters largely supports Greenwood's classification. The necessity to reassign some species should be expected after the first attempt of classifying a complex fauna. Since the characters measured in above cited publications were only part of Greenwood's diagnoses of the genera, the sorting of species into his genera by cluster analysis might even become more complete, if all diagnostic characters would be quantified and used. I do not see evidence for the invalidity of the genera proposed by Greenwood, apart from *Astatotilapia* (see page 235ff). Recently another line of evidence is coming up, that in large produces support for Greenwood's classification: A detailed study of squamation patterns comes to results that are similar to those of Greenwood (E. Lippitsch, in manuscript).

All currently available evidence suggests that Greenwood was more right than not in recognizing phylogenetical lineages among Victorian haplochromines. He may in part have failed to decode his integrated picture of the "general appearance" or "facies" of a lineage, and to quantify its essential components. This can be done now with various multivariate statistical procedures. To understand the evolution of the unique ecological and morphological diversity of Victorian cichlids, we need a picture of phylogenetic patterns amongst them. Greenwood made a first step into this direction. His generic subdivision of the Lake Victoria haplochromines seems not less justified than the generic subdivision of Lake Malawi cichlids and some other cichlid groups. None of these have ever been perfect, but they provide hypotheses that can be tested and altered where needed, to bring forward a more complete phylogenetic picture of cichlid explosive evolution. Personally I feel, to reallocate all species of Victorian cichlids back to one broadly defined genus *Haplochromis*, means a great loss of information. Without giving the doubtlessly existing species complexes formal taxonomic status, they would have remained known only to "insiders". For the majority of other biologists and cichlid hobbyists, however, the Victorian cichlid assemblage would on the paper remain an amorphous collection of species. For these reasons I am in general supportive of Greenwood's classification.

Many of the new species of *Mbipi* can be assigned to the genera *Neochromis* and *Paralabidochromis*. Many others can be assigned to new lineages that were not known by the time of Greenwood's revision. Some of these deserve the same taxonomic rank as the described lineages. In order to give genera similar diagnostic width, the genus *Paralabidochromis*, which was rather broadly defined by Greenwood, and now consists of several large species complexes, may have to be split up. Alternatively, the definition of the genera *Neochromis* and *Xystichromis*, which were narrowly defined by Greenwood, would have to be considerably broadened, and possibly joined, to incorporate several of the new "vertical bar *Mbipi*" lineages. Since this book is not a taxonomical revision, I will present just informal diagnoses of new species complexes, to enable the reader to gain an overview over the diversity of rock-dwelling Lake Victoria cichlids. Pending a formal taxonomical revision of the rock-dwelling cichlids, I opt in this book for a nomenclatorial compromise. In order to provide phylogenetical hypotheses without causing nomenclatorial confusion, particularly among cichlid hobbyists and aquarium fish traders, I use the new generic names as subgenera of *Haplochromi*s until a more definite generic assignment of the new species will be done.

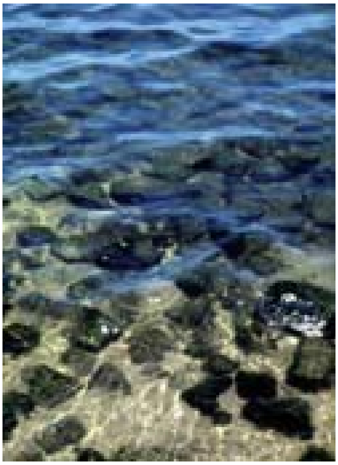
Habitat and ecology of rock-dwelling cichlids

by Ole Seehausen, Anna Samwel-Terry & Niels Bouton

It has not only frequently been assumed that Lake Victoria has few lithophilic cichlids but also that rocky habitats are uncommon in Lake Victoria (Greenwood 1994 as the most recent reference). This view has largely been adopted by aquarists, many of which consider rocks a most typical cichlid habitat in Lakes Malawi and Tanganyika, but muddy and swampy areas as the typical habitats for Lake Victoria cichlids. Certainly are mud bottoms and marginal swamps common habitats in Lake Victoria, and maybe more common than in the other lakes. However, this does not mean that rocky habitats are less common. They are, at least in our research area, in fact just as common as in Lake Malawi. Rocks make up roughly one half of Lake Tanganyika's shoreline (Konings 1988) and about a quarter or a third of the shoreline of Lake Malawi (Ribbink & Eccles 1988, Konings 1995 respectively). Though not yet investigated on its entire length, all available evidence suggests that the shoreline of Lake Victoria is made up by rocks to not less than a quarter either. Stretches of rocky mainland and rocky islands constitute about a third of the shoreline in southern Lake Victoria (text figure 2 on page 17). Rocky shores are very common on the large island archipelagos in the northwestern part of the lake (J.J.M. van Alphen & F. Galis pers. comm.) and in the northeast (L. Kaufman pers. comm.). Even Greenwood himself once wrote that rocky habitats are "not infrequent" along the northern shores (Greenwood 1956a).

A rocky shelf interrupts the swampy shoreline at Bunyago (Mwanza Gulf).

H. "blue obliquidens" grazing algae from a rock.



Small rocks in shallow habitats provide shelter and feeding substrate for small fishes.

Alternating with stretches of sand and small patches of vegetation in sheltered situations, rocky shores form, in the south, a habitat mosaic, very much like that described for Lake Malawi (McKaye & Gray 1984). To somebody travelling by boat along the lake shores, it becomes apparent that the shoreline of Lake Victoria is a drowned landscape. There are old pleisto-

A territorial male *H. nyererei* at Makobe Island at a depth of about 6 metres.

A mouthbrooding OB-female *H.* "blue scraper"

A shoal of plankton-feeding *H. nyererei* at a depth of about 6 metres.

Algae-grazing *H.* "zebra nyererei" (left) and *H.* "blue scraper".

cene river valleys, cut deep into the rocks on one (Speke Gulf) or on both banks (Mwanza Gulf), shallow flooded valleys, hilltop islands like the Vesi Archipelago, and highland ridges like Ukerewe. The substrate at the shore, whether sand, shingle and boulder fields, or steep rock walls, depends on the topography of the drowned environment. The extension of uninterrupted rock shores is very variable. It ranges from less than 50 m to 10 km, but continuous rock shores of more than a kilometre length are rare. There are considerable regional differences in the abundance of rocky habitat. In regions with steep shores like the Mwanza Gulf, the northern Speke Gulf, Ukerewe and Kome Islands, rocks are the dominant shore substrate, frequently interrupted only by small bays with sand bottom, and make up about 50 % of the shoreline. In other regions, like the southern Speke Gulf, sand beaches dominate the shore, and are interrupted merely by rocky peninsulas, so that rocks make up only about 10 % of the shoreline.

The cichlid species found along rocky shores of Lake Victoria have in their majority very specific habitat demands, just like those from Lakes Malawi and Tanganyika. Less than ten of about 80 currently known *Mbipi* species have ever been seen over a substrate other than rock. *H. (Neochromis) nigricans* and *H. (Paralabidochromis)* "rock kribensis" have a few times, *H. (Paralabidochromis) chilotes* and *H. (Paralabidochromis) chromogynos* more frequently been caught over sand, but hardly ever more than 50 metres away from rocks. A species of the *H. (?)* "pseudonigricans" complex (*H. (?)* "grey pseudonigricans" according to Witte et al. 1992) had been observed to leave the rocks by night to forage pelagically on phytoplankton under the surface of open waters 100 to 150 m away from the shore (Witte et al. 1992, Witte pers. comm.). *H. (Xystichromis)* "copper black" can be observed in rock-sand mixed habitats. The other *Mbipi* seem entirely confined to rocky habitats. Similarly narrowly restricted are the depth ranges of many species. For instance *H. (Neochromis) nigricans* and *H. (Neochromis)* "giant scraper" have never been observed or caught at water depths beyond 5 m (Seehausen & Bouton in press).

Due to this extreme stenotopy of the *Mbipi*, stretches of sandy bottom or deep water are effective ecological and geographical barriers to their dispersal. Consequently, populations of one species that inhabit different rocky islands are effectively isolated from each other by deep water. Similarly populations are isolated from each other that inhabit rocky mainland shores, separated by sandy beaches. Migration and therefore gene flow among them is very little and each population evolves largely independently, in response to local regimes of natural selection. If gene flow between them is little enough or completely absent, the populations may evolve into two different species, provided that the external isolation persists long enough. The speed of this process depends on population size, on how different the selection regimes are in the respective environments of the isolated populations, and on incidence. Thus, the combination of extreme habitat stenotopy and patchy distribution of the required substrate, make the *Mbipi* good candidates for micro-allopatric (intralacustrine) speciation (see the chapter on evolution).

The ecology of rock-dwelling Lake Victoria cichlids is further complicated by the circumstance that at any rocky place between 7 and more than 20 different species coexist and share the resources food and space. Before I give an impression of how this is organized, first another look at the rocky habitat. The landscape drowned by the huge water masses of Lake Victoria, is a very ancient one. The dominant rock formation is therefore strongly eroded water- and weather-shaped granite, that exhibits sharp edges only at recent cracks, and is light to medium dark grey in colour. However, at some places black rocks occur, that are more sharp edged and appear less strongly eroded. A third type is a very rough kind of rock, brown-grey in colour and consisting of huge almost continuous units, eroding into boulders of various sizes, that are standing like mushrooms, many at their basis still connected to the "mother rock". We know this type of rock only from the hilltop Mabibi Islands in the central Speke Gulf. Depending on qualities of the underlying rock material, time of its exposure to wind and weather, and topography, rock habitats vary in terms of boulder size and slope. There are huge compact cliffs, as well as big boulders, slabs, heaps and fields of small boulders, stones and coarse pebble, dominating the rocky habitat at different places, and often sharply alternating with each other. At some places extensive horizontal surfaces of very uneven rocky substrate are covered by shallow water, so that outcrops of various sizes emerge from the water surface. Such areas will be referred to in this book as "rock gardens".

Microhabitat characteristics again depend largely on slope and boulder size. A steep precipice of a compact rock wall has little to offer for cichlids. Its surface, as substrate for algae and animal *Aufwuchs*, is much smaller than that of piles of boulders. On top of that, a vertical surface receives less sun light. Thus *Aufwuchs* is less abundant than in habitats with smaller boulders whose surfaces have various inclinations to sun light. Probably even more important, an unstructured rock wall does not offer hideouts for cichlids. Shoals of females and nonbreeding males of plankton eating *Mbipi*, e.g. *H. (?) nyererei* can sometimes be observed in such habitats, but territorial males close to never. On the other end of the range of rocky habitat types are gentle slopes, composed of slabs, small boulders, or pebbles. Here inclination to the sun light is ideal and algae *Aufwuchs* usually plentiful. However, slabs again do not provide hideouts, and are sparsely populated. Among small boulders are many small hollow spaces that serve cichlids as hideouts in case of danger, and that form the centre of every male's territory. In such habitats cichlids occur in large numbers but their ecological diversity is limited because the habitat is rather uniform, the microhabitat diversity is low. Because of the small boulders, there are no large caves, ledges and rocky interstitial spaces, the habitats of crevice- and cave-dwelling cichlids, like the "crevice hunters" of the *H. (Harpagochromis) howesi* complex, and crevice-dwelling species of the *H. (?) nyererei* complex. Furthermore there are no vertical walls along which plankton-rich currents could pass. Plankton eating cichlids therefore do not find suitable conditions either.

The most diverse cichlid communities frequently exist in habitats with medium sized rock boulders. This in especially, when the rocks cover a depth range of at least six meters. Such habitats mostly occur at moderately steep slopes and a representative community has been described by Seehausen and Bouton (1996). The role that the microstructure of the habitat plays in rock cichlid communities, is complex. The availability of territorial space and shelter, and the topographical relationship between these two factors depends on it, but also the composition, diversity, abundance and availability of food. There are two major food resource bases for cichlids at rocky shores: epilithic *Aufwuchs* and plankton. Epilithic (= on rocks growing) *Aufwuchs* consists of a variety of unicellular and filamentous green and blue-green algae, growing directly on the rocks, diatoms that mostly grow on the filamentous algae, moss animals (Bryozoa), Ciliata colonies and sponges. Associated insect larvae and micro-crustaceans living between the algae filaments are often considered part of the *Aufwuchs* as well. Furthermore, different species of snails live on the rocks, grazing the *Aufwuchs*. The zooplankton is dominated by different micro-crustaceans, predominantly species of copepods at the more offshore islands, and species of phyllopods (Cladocera: *Daphnia*) in sheltered shallow water areas. The phytoplankton is frequently dominated by diatoms like *Melosira*, and blue-green algae like the ball-shaped colonies of *Nostoc*. Apart from plankton and *Aufwuchs*, the detritus eating prawns of the genus *Caridina* that have recently increased in Lake Victoria can be a rather abundant source of cichlid food at certain places and seasons (Bouton et al. in press). Other food sources, tapped by rock-dwelling cichlids are snails, *Potamonautes* crabs, eggs, fry and subadults of haplochromines. All these depend directly or indirectly on *Aufwuchs* and/or plankton.

The question about the mechanisms of coexistence and resource sharing in communities of many, closely related species, is a long discussed unresolved problem in ecology. It is a widely accepted rule, known as *Gause's principle*, that two or more species with identical ecological demands, cannot permanently coexist, because one would in the long run be slightly more successful, and outcompete the other one. In order to coexist in the long run, two species must ecologically differ to an extend that allows them to share resources by slightly different specialisations. Thus, they must subdivide an ecological niche into two parts, each utilized by one species more efficiently than by the other one. This phenomenon is known as niche partitioning. In the early days of ecological research on Lake Victoria, scientists got the impression that Gause's principle was violated in cichlid communities (Fryer & Iles 1972, Greenwood 1974). Too extreme appeared the anatomical and ecological similarity among closely related cichlid species, as that one would have thought of ecological niche partitioning among them. However, since then it has been demonstrated on cichlids from habitats other than rocks, that even among anatomically extremely similar species, fine ecological differences exist, that may suffice for successful coexistence (van Oijen 1982, Hoogerhoud et al. 1983, Witte 1984, Goldschmidt et al. 1990).

More recently similar studies have been carried out on communities at rocky shores (Seehausen & Bouton 1996 in press, Seehausen et al. in press [a], Bouton et al. submitted). Rocky areas support more species on less space (higher "species packing"), than do most other habitat types. It was found that each of the different haplochromine cichlids, that coexist at a rocky shore, has its specific and unique niche within the ecological space available to the community as a whole, consisting of specific distribution within the habitat (= microhabitat distribution or microdistribution) and diet. Physical parameters that seem to determine specific microdistribution, are water depth, the amount of shelter in form of caves and crevices, the exposure to wind and waves, and the distance from the shore. Spatial niche partitioning among the members of a rock cichlid community in Lake Victoria exists on a level that is not less refined than that observed among the *Mbuna* of Lake Malawi (Ribbink et al. 1983). It shall be described here exemplary on one island. Species composition, as well as niches of particular species, can differ between localities. Thus, generalizations beyond those that we make, should not be deduced from the following description.

Descending slowly, as a diver, along the moderately steep rocky slope of Makobe Island in the Speke Gulf, one meets first with several species of smaller and bigger algae scraping haplochromines of the *Neochromis* lineage. The highest density of *Neochromis* is found at about 1 to 3 m water depth, but some species penetrate into waters as shallow as 0.5 m (the quieter the water, the further do they penetrate into the shallows). The anatomically very similar species of *Neochromis* have staggered depth ranges, with a trend for bigger species to live in shallower waters. The maxima of the population densities of sympatric *Neochromis* species (e.g. *H. (N.)* "giant scraper" [1], *H. (N.) nigricans* [2], *H. (N.)* "blue scraper" [3], numbers refer to the picture on pages 41) are usually separated from each other by a difference in water depth of not more than one metre. The depth ranges of the species vary between about 3 m and about 6 m. How far the "deepest" *Neochromis* penetrates into deep water, depends on the clearness of the water. Even at clear water islands, however, they hardly go deeper than 6 m.

The fine interspecific differences in depth distribution are accompanied by slight differences in diet, i.e. the proportions of algae and other items, and of different algae types. Though all species the feeding behaviour of which we studied in the labora-

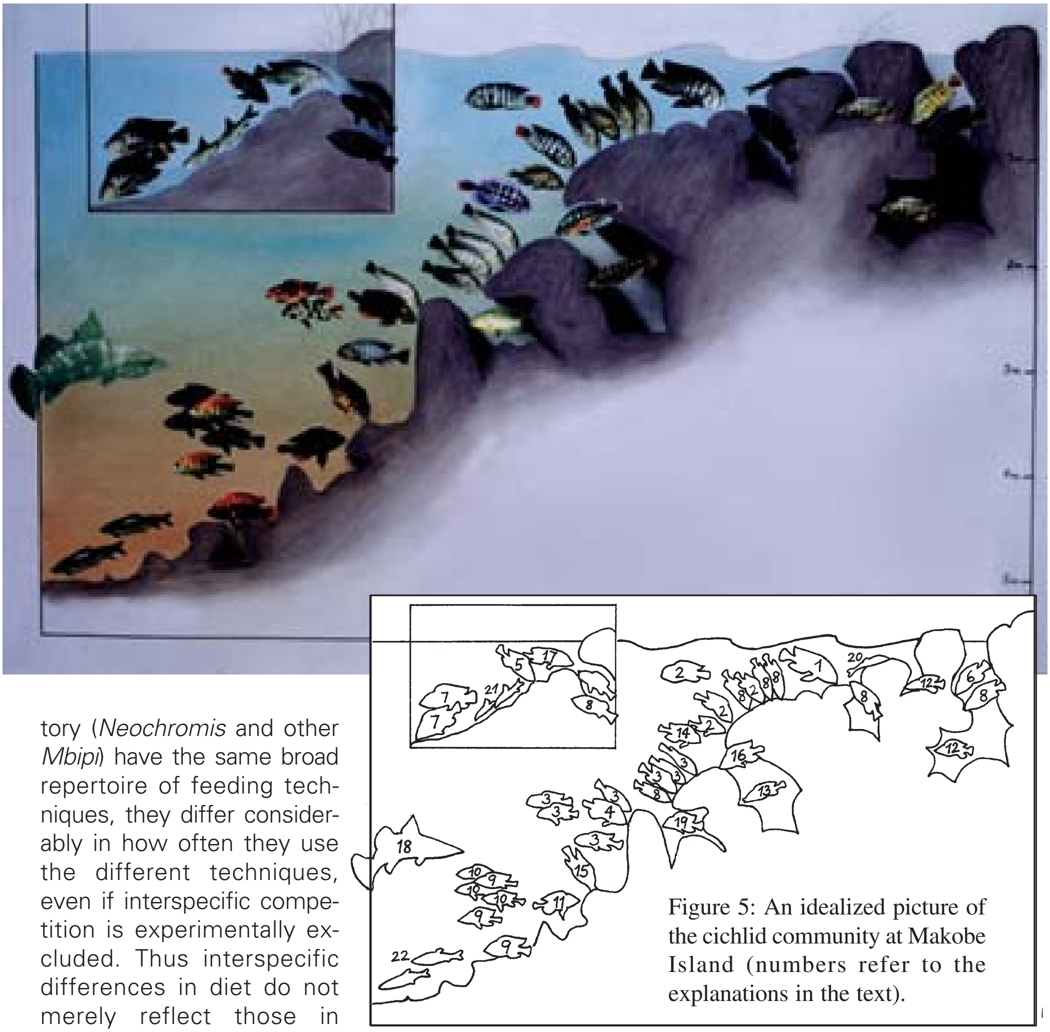


Figure 5: An idealized picture of the cichlid community at Makobe Island (numbers refer to the explanations in the text).

tory (*Neochromis* and other *Mbipi*) have the same broad repertoire of feeding techniques, they differ considerably in how often they use the different techniques, even if interspecific competition is experimentally excluded. Thus interspecific differences in diet do not merely reflect those in microhabitat distribution, but are caused by differences in feeding behaviour as well. All *Neochromis* at Makobe Island feed predominantly on filamentous algae. In the lower part of the depth range of the "deepest" *Neochromis* algae scraper, lives a rare algae scraper of another lineage (*H. (Paralabidochromis)* "short snout scraper" [4]), that feeds predominantly on unicellular diatoms, growing in the less well illuminated parts of the rocky shelf.

A *Cladophora* belt in the wave zone.

A different assemblage of shallow water algae scrapers is found at places where offshore rocks break the waves, so that the shallow water is very quiet. Here species of the *Haplochromis (s.str.)* lineage (e.g. *H. (H.)* "blue obliquidens" [5] and *H. (H.)* "purple yellow"), species of the *Xystichromis* lineage (e.g. *H. (X.)* "carp" [6]), and *Aufwuchs* eating stages of *Oreochromis niloticus*, *O. leucostictus*, and *O. variabilis* [7] mix with the *Neochromis*.

Most *Neochromis* species spend most of their time on the surface of the rocks from which they scrape algae. Another *Aufwuchs* scraper that is more omnivorous lives in the same depth range as those, but more in the interstices between the rocks (*H. (Xystichromis)* "copper black" [8]). However, it is predominantly the male that spends much time in interstices, while the females live like *Neochromis* on the rock surface. Descending to greater depths, one meets at 5 m depth bright red territorial males of *H. (?) nyererei* [9]. Their territories are usually closely spaced and the fishes are frequently involved in some small disputes along territorial boundaries. Only on the second glance the presence of the cryptically coloured females [10] is noticed. They move in shoals across the habitat and remain for some time at spots with high plankton densities. Sympatric with *H. (?) nyererei* live two more planktivorous species, *H. (?)* "pink anal" [11], which has its maximum population density slightly deeper, and *H. (?)* "yellow chin pseudonigricans" which prefers places with somewhat larger rock boulders. Shoals of planktivorous *Mbipi* usually tend to be composed of fishes of relatively uniform size.

Most species in any community occur in much lower densities than the algae scrapers, omnivores and planktivores. These are a number of insect eaters, among which again fine ecological differences exist. The crevice dwelling *H. (?)* "zebra nyererei" [12] and *H. (Paralabidochromis) chilotes* [13] with their shallow head profiles and pointed snouts, feed predominantly on the very mobile larvae of may flies (Ephemeroptera: Baetidae), living on the underside of rocks. In contrast, the steep-headed and short-snouted *H. (Paralabidochromis)* "blue rockpicker" [14] and *H. (P.)* "yellow rockpicker" [15] live exclusively on the rock surface, and feed almost exclusively on the smaller, and less mobile larvae of midges (Diptera: Chironomidae) which live among filamentous algae on the upper side of rocks. Finally *H. (P.)* "rockkribensis" [16] feeds upon larvae of midges and caddis flies (Trichoptera) and has a wider depth distribution than most others.

In very low densities, and without apparent depth preferences, several predatory haplochromines occur in the community. Among them the large *H. (Harpagochromis) serranus* which preys upon small haplochromines, and the paedophage *H. (Lipochromis) melanopterus* [17], preying upon haplochromine eggs and buccal stage larvae, obtained from brooding females. Particularly the species of the deeper parts of the rocky shelf overlap considerably with Nile perch [18] of fish eating size and are a common diet of this predator. Predators that hunt for rock cichlids in shallow water, are little egrets (*Egretta garzetta)*, pink-backed pelicans (*Pelecanus rufescens)* and pied king fishers (*Ceryle rudis*). The catfish *Bagrus docmac*, the spotted neck otter (*Lutra maculicollis*), and cormorants (*Phalacrocorax carbo*, *P. africanus*) do hunt cichlids at various depths. Brooding females of most *Mbipi*, unlike females of many *Mbuna*, guard their fry for a week or more after releasing them for the first time. For this purpose they defend very small territories around a hideout.

In cichlid literature interspecific competition for food resources is sometimes invoked as a mechanism organizing cichlid assemblages, and driving the evolution of apparently highly specialized anatomical forms. The problem with this argument is, that interspecific competition in the African cichlid assemblages has never been unequivocally demonstrated. Some patterns that we found in the spatial and trophic (food related) organization of Lake Victoria rock cichlid communities may indicate that competition among species exists. We have not been able, however, to produce hard evidence.

Evidence for competition for space may be derived from our studies on reproduction. The reproductive ecology of many *Mbipi* is very similar to that of many Lake Malawi *Mbuna*. Reproductively active males occupy territories of between one and several metres diameter. The depth ranges, across which territories are distributed, are quite similar to the usual foraging depth ranges of the species. Thus, in any given depth, several species reproduce in sympatry (Seehausen 1996d, and unpubl. data). Territorial densities can be extremely high. Males often defend their territories not only against males of their own species but also against those of other species, so that interspecific competition for territory sites may exist among them. Patterns of geographical and microdistribution in some species pairs are suitable to lend support to this hypothesis. So does the microdistribution of territories of *H. (?)* "blue nyererei" at different islands in the Speke Gulf correlate with the absence or presence of *H. (?) nyererei* (see page 119).

Apart from showing that each species in the complex communities of rock-dwelling cichlids has its unique combination of microhabitat, behaviour and diet, our studies show that these communities are relatively stable but not static assemblages. Environmental fluctuations have considerable impact on the degree of ecological niche partitioning, thus on the magnitude of ecological difference among species. Niche differences can be largely reduced at times of high abundance of one food item, when most species prey heavily on it (Bouton et al. submitted), and at times of low water levels, when spatial overlap among species increases (Seehausen & Bouton in press). This implies that the complex communities of rock cichlids are very sensitive to fluctuations in the environment.

Keeping and breeding rock-dwelling cichlids

Nothing is more beautiful than a large rock aquarium with a group of *Haplochromis nyererei* whose fire red males dance like butterflies around the females, with sky blue male *H. (Neochromis)* "blue scraper" and yellow, orange blotched and piebald females, busy scraping algae from rocks, with a few deep yellow females and orange-red males of *H. (Paralabidochromis)* "rockkribensis", and with some *H. (Paralabidochromis) chilotes*, digging with their over-dimensional lips in the sand among the rocks.

In spite of their beauty, very little has been published about aquarium maintenance of rock cichlids from Lake Victoria, compared to the extensive literature that is available about those from Lakes Malawi (Nyasa) and Tanganyika. Victorian rock cichlids, with few exceptions, have just recently become available to hobbyists. A few species, such as *H. (Neochromis) nigricans* and *H. (?) nyererei* have been in the hobby for quite some years now. However, a few species, "isolated" from their taxonomical, ecological and evolutionary context, are not enough to establish and keep busy a lobby among cichlid enthusiasts. This in particular, since information about Lake Victoria rock cichlids was not available, neither in aquarium literature, nor in scientific literature. With the many new discoveries along rocky shores, and the upcoming trade with Victorian cichlids, this picture is now changing. About 50 rock-dwelling species are already maintained in aquaria (table 1). The first articles about rock cichlids are appearing in aquarium journals, though those among them that describe first-hand experience with keeping and breeding, are still the exception (e.g. Schraml 1990, Raymond 1995, Boehme 1996). Unfortunately some pioneering au-

A male *Haplochromis* "crimson tide" in the aquarium.

A pair of *Haplochromis chilotes* in the aquarium.

Fighting males of *Haplochromis chilotes*.

An OB-female of *H*. "blue scraper" from Makobe (left) and a male *H*. "red pseudonigricans".

A male *Haplochromis chilotes.*

thors do explicitly or implicitly assume that their experiences with some Victorian cichlids are applicable to most. Such wrong generalizations were made also about Malawi and Tanganyika cichlids when the first species entered the hobby, implying that Victorian aquaristics is still in its infancy.

Understanding of taxonomy and ecology of Lake Malawi and Tanganyika cichlids would certainly be far less advanced without the many valuable observations made by cichlid hobbyists, which consequently fuelled scientific research. What is needed to achieve a similar participation of aquarists in the accumulation of knowledge about Lake Victoria cichlids, is literature to provide the upcoming hobbyist lobby with background information about identification, taxonomy, ecology and the natural environment of their new clientele. Though this book is mainly aiming at giving this information for rock cichlids, I want to give a brief introduction to aquarium keeping and breeding, which will at places expand beyond the species that live at rocky shores.

The aquarium

Aquariums for Victorian cichlids can be as diverse as the cichlids. The minimum aquarium size, however, should not contain less than 80 litres water. Such small aquaria, if equipped with a good filter, are perfectly suitable to keep and breed small sublittoral and pelagic zooplanktivores, such as *Haplochromis (Yssichromis) pyrrhocephalus*, *H. (?) piceatus* and *H. (?)* “argens”. The wide spread belief that Victorian cichlids are very aggressive, is based on one of the many wrong generalizations. These pelagics, that are in some ways similar to *Cyprichromis* from Lake Tanganyika, exhibit very little intra- and interspecific aggression. Many (not all) rock-dwelling cichlids, however, are potentially quite aggressive. This holds mainly for the “Vertical bar” and “Chessboard *Mbipi*” (*Neochromis* and *Xystichromis* lineages, Nyererei-, “Deepwater”-, and “Pseudonigricans”-complexes, *Paralabidochromis* lineage). However, their aggression is the result of keeping mistakes, and can be overcome by some tricks.

To successfully maintain rock cichlids, aquaria should be 1.5 m long or longer and contain 250 litres water or more. With some experience, groups of one male and several females can be successfully kept in aquaria of 1 m length and 160 litres volume, but this deserves careful observation, in order to be in time to intervene if the social balance in the group tilts. Anybody who has observed Victorian rock cichlids in their natural environment or in big aquaria, knows that these fishes are territorial but not really aggressive. Serious territorial disputes are rare in nature, and I have never seen real fights between males. Neither do males in nature engage in aggressive behaviour against brooding females. Territories of *Mbipi* males have between less than 1 and several metres diameter, depending on the species and the size of a male. It is simply the space limitation in small aquaria that makes them aggressive. It does not allow rock cichlids to establish territories of adequate size, and worse, it does not allow submissive individuals to leave the territory of a dominant one. Resistance of an intruder against leaving somebody's territory, would in nature most likely indicate that it does not accept the dominance of the territory owner. Consequently the latter would continue to display its dominance until the intruder leaves. In an aquarium that is too small to provide extraterritorial space for subdominant individuals, this must lead to a catastrophe. Therefore, to begin with rock cichlids, I would strongly advice an aquarium of not less than 250 litres volume.

The interior of the aquarium can be very important to ensure peace among the fishes. Mistakes in this regard are one of the most common reason for loss of fishes. A few “hideouts”, say five or ten rock caves or flower pots, usually help nothing to protect submissive individuals against the attacks of a dominant tank mate. As long as the latter can enter "hideouts", it will be very consistent in searching each, until it has found the submissive fish, that apparently does not "want" to leave the territory. The territory owner will soon be so experienced in patrolling each "hideout" that the submissive fish will get no rest anywhere in the aquarium. There are a number of possibilities to avoid this. In cases where the aggressor is much bigger (deeper bodied) than the inferior individuals, enclosures can be provided with small entrances that allow only the smaller fishes to pass, and make them real hideouts for them. Among rock cichlids this can often be helpful to protect females against male attacks. In most rock cichlids, and particularly in the strongly territorial algae scrapers of the *Neochromis* and *Xystichromis* lineages, males grow distinctly bigger than females. Such real hideouts can be PVC tubes or broken flower pots that are pressed into the sand so that one or (better) several openings exist that allow only the females to enter. Better of course are more spacious hideouts if provided with the respective small openings.

If the females are not smaller than the male, or if more than one male are to be kept in one tank, the most promising solution to overcome problems with aggression, depends on the relationship between aquarium size and fish group size. If the group consists of ten or more individuals, either large parts of the aquarium should be covered by complex structures of rocks, creating tunnels and gaps of various sizes, and separating the aquarium into several compartments by visual barriers, or the aquarium should have no hiding places at all. If a larger number of fishes in an unstructured aquarium continuously see each other, the aggression of dominant individuals will be spread more evenly over the others, and males become in such situations not strongly territorial. This is usually the safer solution in relatively small aquaria. However, it does not function if group size is small because the aggression cannot be spread over many enough individuals, and abuse of the weaker fish will be the consequence. Even if group size is large, the behaviour of the fishes cannot be reliably predicted, and careful observation is needed, in particular during the first days after setting up a group.

Nevertheless, also small groups of one male and two or three females, even pairs, can be kept successfully if the "dither fish method" is applied. Dither fish are fishes of other species that are introduced to help divert the attention of the male, and to disperse its aggression. Dither fish can be any fish that are tough enough to receive attacks of a haplochromine male, and not strong enough to chase him away from his territory. I made good experience with small groups of subadult tilapias or females of other haplochromines. In the latter case only such species must be used that cannot be confused later with the females of the species to be bred.

It should be stressed, that not all rock-cichlids are equally aggressive. I am keeping and spawning a group of two full grown males and three females of the paedophage *H. (Lipochromis) melanopterus* since more than a year in a 160 litres aquarium without dither fish. The dominant male is that little aggressive that I never had to remove brooding females, hardly ever saw them being chased away even from the close vicinity of the male, and never found their fins or scales damaged, nor those of the second male. Also *H. (Lipochromis)* "matumbi hunter" and *H. (Harpagochromis)* "orange rock hunter" are very little aggressive, and it seems that predatory cichlids are on average less aggressive than algae scrapers and rock-dwelling insect eaters.

If aquarium size and cichlid group composition allow to structure the aquarium, rocks of different sizes should be piled up against the back side and at least one lateral side of the aquarium. The bottom can be filled up with gravel. However, if one wishes to observe male haplochromines constructing their spawning pits, sand should be used instead of gravel. Nevertheless, caution is needed that the rock piles are very stable, and cannot be undermined by digging. It is advisable to fix at least the lower layer of rocks with silicon on the aquarium ground. Spawning pits are usually dug out under overhanging rocks! In their natural environment, territorial rock cichlid males have several hideouts in their territory which they know very well, and into which they flee in case of disturbance. These hideouts generally are crevices among the rocks. Males of Victorian rock cichlids have a considerable demand for "security", and are in the aquarium more shy than females, just like Konings (1995) observed among rock cichlids from Lake Malawi. To meet these demands, it is very important to paint the background, and maybe one or both sides of the aquarium with dark colour. If light falls into the aquarium from behind, caves among the rocks will not be dark, will not be considered "caves" by the fish, and will not contribute to their feeling of security. Colourless fishes will be the consequence. This should be taken very serious because Lake Victoria haplochromines, more than those from Lake Malawi, can lose all their colours within minutes or hours. They become then totally unsightly. This is one reason why Victorian cichlids rarely look attractive in the tanks of traders and pet shops.

Plants rarely grow in the natural habitat of most rock-dwelling cichlids. Nevertheless, some hardy species are suitable to make a rock cichlid aquarium more attractive. *Vallisneria*, *Ceratophyllum* and *Najas* are frequently found in sandy and muddy littoral habitats of Lake Victoria. At least the first two are suitable for a rock cichlid aquarium. I also have very good experience with *Bolbitis* and *Microsorium* ferns and with *Anubias*. None of them grows in Lake Victoria but they are particularly suitable in an aquarium with cichlids that dig much, such as *H. (Paralabidochromis) chilotes*. One can simply fix them on, or among rocks, and after a few weeks they will get with their roots attached to the rocks. In aquaria with smaller, and not much digging haplochromines, I made good experience also with *Cryptocoryne affinis*. Some Victorian haplochromines eat plants. Among those discussed in this book, it is mainly *H. (Haplochromis)* "purple yellow" and maybe other members of the *Haplochromis* lineage *sensu stricto*, *Astatotilapia nubila* and probably some species of the *Neochromis* and *Xystichromis* lineages. However, also these do not eat all plants. They hardly ever touch *Bolbitis* and *Microsorium*, while they can finish *Vallisneria* down to the roots.

Water and food

Concerning water chemistry, Lake Victoria cichlids do not have particular demands. The water in their natural environment is usually rather soft, the pH neutral to alkaline. In the aquarium it is difficult to keep soft (bicarbonate poor) water at a neutral to alkaline pH, because of its low buffer capacity. Most Victorian cichlids thrive and breed perfectly in somewhat harder water. In regions with soft and acidic tap water, it is advisable to improve buffer capacity by putting a limestone into the aquarium and adding sodium bicarbonate, as described by Forsberg (1993). In recently set up aquaria that do not yet have a functioning flora of nitrifying bacteria, as well as in overcrowded, mechanically filtered rearing tanks that anyway hardly get such flora, problems with nitrite accumulation are commonly encountered. Some Victorian cichlids are more sensitive to it than others. Open water dwellers and rock cichlids are generally more sensitive than inhabitants of muddy bays and submerged vegetation. Nitrite at higher concentrations blocks the oxygen uptake of fish. Fish suffering from nitrite intoxication breath heavily without ascending to

A male *Astatoreochromis alluaudi* from an aquarium population.

the surface as they would do in case of suffocation. Immediate change of 50% of the aquarium water usually helps. Additionally it can be useful to stop feeding for a day or two to interrupt the supply of nitrogen. We experienced very different levels of sensitivity to organic water pollution, when, at the Tanzanian fisheries research institute in Mwanza, we failed to maintain cichlids in water from the Mwanza Gulf, that were caught in the relatively clean waters of the open lake. Detailed information about filter systems for cichlid aquaria is given by Fohrman (1993a) and Bailey (1993).

In a recommended article about keeping and breeding of Victorian cichlids, Raymond (1995) rightly complained that no popular text existed that would provide information about what the individual species of Lake Victoria cichlids eat in the wild. Information about the diet of various rock-dwelling cichlids is provided in other chapters of this book. Though not actually a popular text, a publication of Witte & van Oijen (1990) contains easily understood information on the diet of Victorian cichlids from other habitats, which is very useful for aquarists. In aquaria, Victorian cichlids are usually not choosy. Coming from the wild, many species have initially some difficulties in accepting flake food. With white and black mosquito larvae I always succeeded to get them start eating. Later they usually accept also flakes. In composing the aquarium diet of Victorian cichlids one should, to some extend, consider the natural diet of the different species. The most commonly made mistake in feeding haplochromine cichlids is to offer minced meat or cattle heart. Cichlids should never be fed with mammal products because they cannot assimilate the fat of warm blooded animals. The consequence is liver adiposis which earlier or later leads to death. A recommended text on cichlid feeding has been written again by Fohrman (1993b). In the keeping and breeding system of the Institute of Evolutionary and Ecological Sciences in Leiden, we have good experience with keeping various species of Victorian cichlids on minced prawns as the staple. It is important that the chitin shells are not removed before mincing the prawns.

They are important as bulkage in the digestive tracts of the fishes.

For herbivorous species, like *Neochromis*, *Xystichromis* and *Haplochromis (sensu stricto)*, vegetative matter should form part of the diet. In a well illuminated and sparsely populated tank, green algae growing on the rocks can do. In most situations, however, additional vegetative food, e.g. spinach or peas will be required. I made good experience with algae covered stones from local lakes that I exchange every three to four weeks. However, one should be aware of the possibility to introduce fish parasites in this way. Alternatively one can, at least during the summer months, keep some stones in a shallow water basin in the garden until they are overgrown by green algae. This can take a while, and the *Aufwuchs* will never be as diverse as that on stones taken from a lake, but the danger of introducing fish parasites can be avoided this way. Personally I prefer to feed algae scraping cichlids with algae covered stones, rather than with peas and spinach only, because it offers a possibility to observe their natural feeding behaviour. Algae scrapers, more than others, will not prosper on a diet that consists exclusively of easily digestible, protein-rich food, such as mosquito larvae or brine shrimps. They may soon suffer from intestinal bloat.

To observe their natural way of feeding, it is most rewarding to offer living snails to snail eating haplochromines. Most species of *Ptyochromis*, as well as *Macropleurodus* and *Platytaeniodus*, even if well fed on other food, readily take to snails as soon as they are thrown into the aquarium. Though I have not tried it, I think that a few individuals of any of these cichlids are perfectly suitable to control a snail plague in an aquarium with other fishes. However, they prefer planorbids, and I never saw them eating *Melanoides* snails. The latter are eaten by some snail crushers, e.g. by *Astatoreochromis alluaudi*. When my stock of snails is exhausted, I use to add marine bivalve meet to the food of snail eaters. Meet of *Mytilus* and *Edulis* is equally well eaten, though most fishes need to get accustomed to its taste and rather strong flavour. All snail eaters can be fed with minced prawns as a staple.

Fish eating predators and large insect eaters have successfully been kept on a mixed diet of prawns, bivalve meet and trout pellets (make sure they contain neither meet nor fat of mammals or birds). From time to time I feed piscivores with juvenile cyprinids (bream and rouche). If no live fish is available, small pieces of cod are also eaten. Copepods are a very good food for all smaller haplochromines. Feeding the anatomically specialized pelagic zooplankton eaters with living copepods will allow the observer to admire the widely protractile sucking mouth of these tiny cichlids. Finally the usual advice to any fish keeper: Do not overfeed. Do not give more than can be eaten within two minutes, and do this not more often than twice a day.

Breeding

Breeding of Lake Victoria cichlids is usually, but not always, easy. As far as known, all species are female mouthbrooders without pair bond. Nevertheless, a potential for male mouthbrooding exists at least in some species. I observed a complete sequence of mouthbrooding over six weeks in a male *H. (Harpagochromis)* "orange rock hunter". To breed rock cichlids, one should ideally start with a group of one male and five or more females. Regrettably this will rarely be possible because haplochromines are mostly still sold in pairs. Not many people will be able, or even wish to afford purchasing five pairs, in order to keep four of the males in a separate tank. In such cases, I suggest to start out with a pair in the following way: Do not put them straight pairwise into the spawning tank. Instead keep them separate (the female in the spawning tank) until the female's abdomen is swollen of eggs, and her genital papilla well visible in lateral view. Bring then the male, together with some dither fish, into the spawning tank (if you do it the other way round, and bring the female to the male, the latter is usually more aggressive because it considers the female a territorial intruder as soon as she is not ready to spawn). Observe the pair. If the female follows the courting male on his lead swimming (see below), things may go well. However, continue to keep an eye on them and be ready to separate them again if you see that the female is not yet ready to spawn and is being chased aggressively. The aquarium should contain some hideouts for the female. Dense stands of *Bolbitis* or *Cryptocoryne* sometimes do wonders and can make it possible to leave pairs together even if the female is not yet ready to spawn. Never use male haplochromines of other species as dither fish. They may fertilize eggs of your female even if they are dominated by the male of the breeding pair (see below). In my aquaria even such different species as the pelagic zooplankton eating *H.* "argens" and the bottom dwelling snail sheller *H. (Ptyochromis) sauvagei* hybridized without difficulty. After spawning has happened, the male and the dither fish should be removed.

If the pair does not spawn within 24 hours, you should remove the male and try it again after a couple of days. If then they still do not spawn, most likely the eggs of the female are not ripe yet. You have to separate the pair again, keep particularly the female on optimal diet, and try it again after some time. If this method does not work, you can try to keep your pair permanently with a group of females of other haplochromines. The older the fishes become, the more difficult will it become to spawn them. Once breeding with a pair was successful, a larger breeding group should be assembled from the offspring. From then on things usually go much easier. However, if you can, try to spawn the pair several times, and compose a breeding group from several nests, to keep up genetic diversity. If enough fishes are available Victorian cichlids should never be kept in pairs or small groups for spawning. The bigger the group, the better. Larger groups of most rock cichlids spawn without any particular action on the part of the care taker.

Table 1: Rock-dwelling Lake Victoria cichlids of which aquarium populations exist

***Mbipi* species**	**other rock-dwelling species**
H. (Neochromis) "black nigricans"	*Astatoreochromis alluaudi*
H. (Neochromis) "blue scraper"	*Astatotilapia nubila*
H. (Neochromis) "cross dresser"	*H. ("Astatotilapia") brownae* ?
H. (Neochromis) "giant scraper"	*H. (Haplo.)* "blue obliquidens"
H. (Neochromis) nigricans	*H. (Haplochromis) lividus* ?
H. (Neochromis) "red anal nigricans"	*H. (Haplo.) obliquidens* ?
H. (Neochromis) "unicuspid scraper"	*H. (Haplo.)* "red back scraper"
H. (Neochromis) "velvet black"	*H. (Harpago.)* "orange rock hunter"
H. (Xystichromis) "carp"	*H. (Harpagochromis) serranus*
H. (Xystichromis) "copper black"	*H. (Labrochromis)* "stone"
H. (Xystichromis) "Jinja blue scraper"	*H. (Lipochromis)* "matumbi hunter"
H. (?) "big blue" (blue) (*Nye*)	*H. (Lipochromis) melanopterus*
H. (?) "black & orange nyererei" (*Nye*)	*H. (Psammochromis) riponianus*
H. (?) "crimson tide" (*Nye*)	*H. (Psammochromis) saxicola*
H. (?) nyererei (*Nye*)	*H. (Ptyochromis) sauvagei*
H. (?) "red head nyererei" (*Nye*)	*H. (Ptyochromis) xenognathus*
H. (?) "zebra nyererei" (*Nye*)	*H. (?)* "double stripe" Uganda
H. (?) "deepwater" (Dwa)	
H. (?) "blue pseudonigricans" (Png)	**occasional intruders from other habitats**
H. (?) "pseudonigricans" (Png)	
H. (?) "Hippo Point blue bar" (?)	*H. (Macropleurodus) bicolor*
H. (Paralabidochromis) chilotes	*H. (Prognathochromis) perrieri*
H. (Paralabidochromis) plagiodon	*H. (Yssichromis ?) piceatus*
H. (Paralabido.) "rockkribensis"	*H. (?)* "argens"
H. (Paralabido.) "blue rockpicker"	*H. (?)* "citrus" ?
	H. (?) "thick skin"

(Nye) = *H. nyererei* complex, (Dwa) = *H.* "deepwater" complex, (Png) = *H.* "pseudonigricans" complex

Photos 1 to 9: A spawning sequence of *Astatotilapia nubila* in the aquarium. See text for explanation. Photo 10 to 12: A male "exchange" during spawning. While a pair *A. nubila* spawns (10) a male *Thoracochromis sp*. attacks the *A. nubila* male (11), chases it away and continues spawning with the *A. nubila* female (12).

The mating of Lake Victoria cichlids in gross follows the ritual described for other haplochromine cichlids with fertilization of eggs in the mouth of the female. However, differences in details exist between different ecological groups. In all species the male attracts a ripe female by *lateral display*. For this purpose he usually approaches or overtakes the female and presents his beauty laterally in front of her, stretching all his fins. Some cave dwelling rock cichlids hardly leave the entrance to their cave while performing lateral display, trying to attract females on larger distance. If the female does not escape, or if she approaches the male in case of "cave entrance courtship", the male's lateral display merges into *quiver*. A shaking runs across the male's body, while the spinous part of the dorsal fin is folded, the anal is stretched and the caudal fin bent away from the female. Quivering merges into *lead swimming* if the female has not moved away yet. While leading her to the nest, the male performs waving tail beats. On the nest the male performs a *loop* and returns to the female to repeat the procedure. The female follows usually only stepwise. Once the female reaches the nest, the male attains *T-position*, placing himself horizontally in front of her head, and presents his anal with the egg dummies pressed against the bottom of the spawning pit. The T-position can be followed by some rounds of *circling*, during which the partners turn around each other with their vents on the bottom of the pit, and during which no eggs are laid yet.

If up to here everything went well, the female at some point drops a few (1-5 but usually 2 or 3) eggs and immediately turns to pick them up. While she picks them up, the male resumes T-position, presenting his egg dummies just next to the real eggs. After having collected her real eggs, the female picks at these dummies, the male releases milt, and the eggs are fertilized in the female's mouth. The male then turns, and touches with his mouth the anal region of the female, apparently stimulating her to spawn more eggs. This sequence of acts is repeated until the last eggs have been spawned and fertilized. Spawning is in nature frequently interrupted by disturbance. When the male has to chase away intruders, the female usually remains in the nest, waiting for him. However, I have observed females leaving the nest in such moments, to continuing spawning with another male elsewhere!

In some pelagic Victoria haplochromines, the ritual that leads to spawning, can deviate slightly from the above described one. Lead swimming to the bottom rarely occurs. Instead the pair can assume T-position in the water column and sink down to the bottom in this position. Once a female of the pelagic *H. (Yssichromis) pyrrhocephalus* was seen spawning some eggs in the water column (F. Liczkowski pers. comm.). However, only aquarium observations are available yet on courtship and spawning of pelagics, and even these are few.

As stated above, spawning of Victorian rock cichlids is most successful in a larger group. Since it will often not be possible to remove all other fishes after a pair has spawned in a large group, brooding females at some point have to be removed from the community aquarium. This can be a most difficult task, particularly with rock cichlids, spawned in a well structured rock aquarium. Brooding females do usually not respond to bait and cannot be caught in baited traps. In most cases there will be no way to avoid disassembling the rocks to get the female. However, before this is done, it is sometimes useful to try to catch her by surprise. A brooding female that moves around with the other fishes and does not hide, can sometimes be caught by one fast and well targeted movement with the hand net, e.g. during feeding of her tank mates. If this goes wrong and the rock piles have to be disassembled, it proved very helpful to manipulate the brooding female into one corner of the aquarium, and block that part of the aquarium with a PVC board. The remainder of the aquarium can then stay undisturbed.

An important question is when to remove a brooding female from the community aquarium. I have negative experience with doing this shortly after spawning. Females frequently jettison (rather than swallow) their eggs in the net or after being released in the new environment of the brooding tank. Females that have already been brooding for some days, are less likely to jettison their eggs or fry. Females of most rock cichlids generally hold their clutch better than females of, for instance, pelagic zooplanktivores. To ensure a good timing of the removal of brooding females, knowledge about the incubation time is needed. Remarkably little, not to say nothing, has been published about this aspect of reproduction biology in Victorian haplochromines. My data are not many but they are sufficient to show that incubation period (defined here as time between spawning and the first release of the fry) and post buccal care duration (defined here as time between first release and last guarding of the fry) are worth looking at more carefully. Though incubation period depends also on water temperature, both incubation period and post-buccal care duration are, at equal water temperature, very different among different species. Some examples are given in table 2. My experience is that the best time to shift a brooding female into a nursery tank, lies between the beginning of the last third of the incubation period and three days before the expected date of release. Attempts to shift a female too shortly before the release of the fry can sometimes lead to a panic release before the female is caught.

As nursery, a 50-litres aquarium is sufficient, furnished with a heater, a sponge filter and a hideout for the mother. A hideout in a nursery should not be too small and should be easy to look into. In nature brooding females of rock cichlids defend small territories around a rock hole. Never put more than one female into one nursery tank. They can become very aggressive, particularly after the first has re-

Table 2: Approximate duration of parental care of some Lake Victoria haplochromines.
Determined at temperatures between 24 and 26°C in aquaria.

	days until first release of fry (mean)	additional days until last mouthing *
Vertical bar *Mbipi*		
H. (Neochromis) nigricans	21	up to 21
H. (Neochromis) "unicuspid scraper"	20	up to 20
H. (Xystichromis) "copper black"	21	up to 21
H. (Xystichromis) "carp"	21	up to 17
H. (Xystichr.) "Uganda blue scraper"	21**	?
H. (?) nyererei	21	7
H. (?) "zebra nyererei"	21	7
Chessboard *Mbipi*		
H. (Paralabidochromis) chilotes	15	up to 20
H. (Paralabidochr.) "rockkribensis"	18	2
H. (Paralabidochr.) "blue rockpicker"	15	up to 15
rock-dwelling fish predators		
H. (Lipochromis) melanopterus	20	up to 38
H. (Lipochromis) "Matumbi hunter"	?	20
H. (Harpagochr.) "orange rock hunter"	21	21
others		
H. (Ptyochromis) sauvagei	21	7
H. (Haplochromis) "blue obliquidens"	22	up to 6
Astatotilapia nubila	18	up to 28
pelagics		
H. (Yssichromis) pyrrhocephalus	13.5	1-2
H. ("Astatotilapia") piceatus	15	1-2
H. (?) "argens"	22	1-2

* maximum values are given; up to *n*, indicates large variability

** from Selbrink 1985a

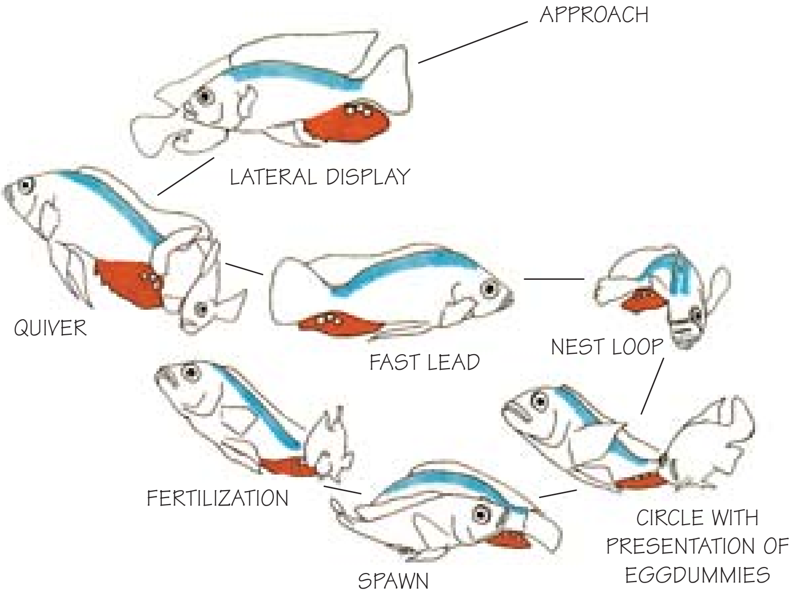
leased her fry. Females of a few species (e.g. *H. (Harpagochromis)* "orange rock hunter") continue to eat during mouthbrooding. They suck the food into the mouth, which they open just a tiny gap wide, while the eggs or fry are kept far behind in the buccal cavity. However, in most species brooding females are apparently unable to suck in food while brooding (I have not tried with plankton yet) and should during this time not be offered food to prevent water pollution. Feeding must be resumed as soon as the fry is released for the first time.

The size of the fry at the time of first release is not uniform among species, but the fry of most species are large enough to eat brine shrimp nauplii, microworms and crushed flake food. Those of pelagic zooplanktivores are particularly big, in spite of the short incubation times of those species. The fry of vertical bar *Mbipi* is usually also rather big, those of chessboard *Mbipi* tends to be smaller. The smallest fry I have seen, were those of the snail sheller *H.* (*Platytaeniodus) degeni*, which were unable to handle crushed flake food and starved when no brine shrimp nauplii were fed. After refraining from brood care, a female should be removed from the nursery and get the opportunity to rest and recondition before she is brought back into a tank with a male.

Clutch sizes among Victorian haplochromines vary in nature between as few as 13 eggs in some pelagic zooplanktivores and 170 in *Astatoreochromis alluaudi* (Goldschmidt & Goudswaard 1989). Juveniles grow slowly and reach sexual maturity at an age of between six months and a year. Already somewhat earlier one can often tell females and males apart. However, in most species some individuals develop their secondary sexual characters very late. The maximum life expectancy of Victorian haplochromines under good aquarium care is about three years.

If you want to reproduce your fish and maintain the different species, do not breed them in community tanks with males of more than one haplochromine species. Females are usually choosy during courtship, and select their own males, if these are available (if not, they spawn with any male). However, once a female is in the nest and has started spawning, she can loose her choosiness and continue spawning even if a male of another species has chased away her male, and has taken over his position (see photo series). This can happen, if the owner of a territory was just slightly dominant over another male, and if this instable dominance relationship tilts during spawning when the other male starts to fight for the nest with the female in it. However, even a clearly dominant male can often not prevent others from fertilizing some eggs of "his" female by *sneaking* into his nest during spawning. Sneaking is most successful if sneakers are much smaller than the territorial male.

Astatotilapia nubila



Haplochromis pyrrhocephalus

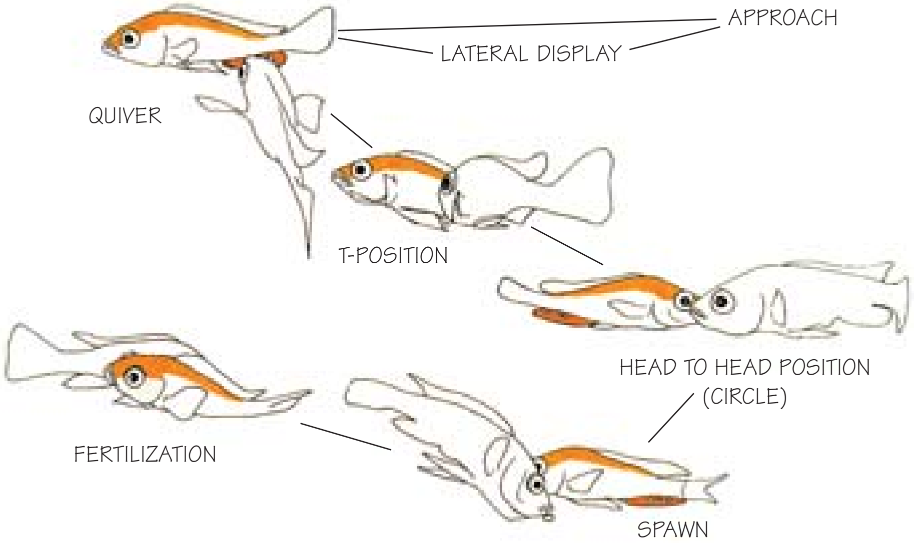


Figure 6: Elements of courtship behaviour and spawning in two Lake Victoria haplochromines: the benthically living *Astatotilapia nubila* (above) and the pelagically living *H. (Yssichromis) pyrrhocephalus* (below). Drawings made after photographs. Most rock-cichlids court and spawn similar to *A. nubila*.

Identification of rock-dwelling haplochromines

That identification of haplochromine cichlids from Lake Victoria can be quite complicated is becoming apparent if one considers that more than 70 % of the species, featured in European and American aquarium literature, were shown under wrong names. This rate lies certainly much above the average for cichlids, and is probably partly due to the lack of popular identification literature, but partly to the misunderstanding of the importance of coloration in species identification. Coloration is very important for the identification of Victorian cichlids, but only in combination with other morphological characters. Attempts to identify species only by coloration are frequently bound to fail. Very similar colour patterns occur repeatedly in Lake Victoria among species of different taxonomical and ecological groups. A typical example is black body with red anal and caudal fin and dorsal fin rim, found in *Astatotilapia*, *"Astatotilapia"*, *Xystichromis*, *Neochromis*, *Haplochromis* and the "Deepwater" complex. Most fishes with such coloration are erroneously "identified" as *A. nubila* in popular literature. For any reliable identification, some anatomical characters have to be investigated. When this has resulted in the identification of the ecological and/or taxonomical group a species belongs to, coloration may be of great value to complete the task to identify it to species level.

To investigate some taxonomical characters is not as difficult as some cichlid hobbyists fear, and quite something can be done on the living, anaesthetized fish without causing it much harm. I hope that the identification key presented below, will aid in this. The key does not go down to species level. Compiling a species level key to haplochromine cichlids of Lake Victoria, is a basically infeasible task. However, it was also for other reasons not desirable at this point. Some "new" species of rock-dwelling cichlids are currently being discovered on every expedition into an area, that was not sampled previously. This would render a species level key an only locally useful tool. Instead, I provide here merely some help for the identification of the major species complexes and (sub)genera that make up the cichlid communities of rocky shores in Lake Victoria. Most of the "new" species that are to be expected within the coming years, will probably belong to these species complexes. Thus, the key may retain some relevance, though the discovery of more species will certainly quantitatively, and maybe also qualitatively, change the group characters and their ranges (see the chapter on taxonomy).

The key, addressing cichlid keepers and breeders as well as field workers, uses only characters that can be measured, counted, or observed on a living, anaesthetized fish. However, a binocular microscope will be required, and at one place in the key an otoscope, to look into the throat of a fish. This key differs from the simple dichotomous one that taxonomists usually wish to have. Like other authors before (Greenwood 1973, 1980, Snoeks 1994), I found it impossible to compile such a key. Differences among haplochromine species and species complexes can often not be pinned down to a single character. Rather it is in many cases the combination of characters that sets one group apart from another one. Each of these characters exhibits considerable individual and intragroup variation, so that often more than one character have to be consulted to separate two groups.

Ranges of morphometric measurements used in this key, are ranges of mean values of the species that make up the keyed out species complexes. Ranges of individual variation are larger, are strongly influenced by extreme individuals that exist in any larger sample of Victorian haplochromines, and depend therefore much more than means on incidental sample composition. The consequence is that this key is not suitable to identify a single individual, though it may in cases key out correctly. Rather it is meant for the identification of samples of at least three individuals, so that some idea about variation can be achieved, and means for morphometric values can be calculated. Nevertheless, because of the extreme individual variability of many Lake Victoria haplochromines, even if this is kept in mind, the key

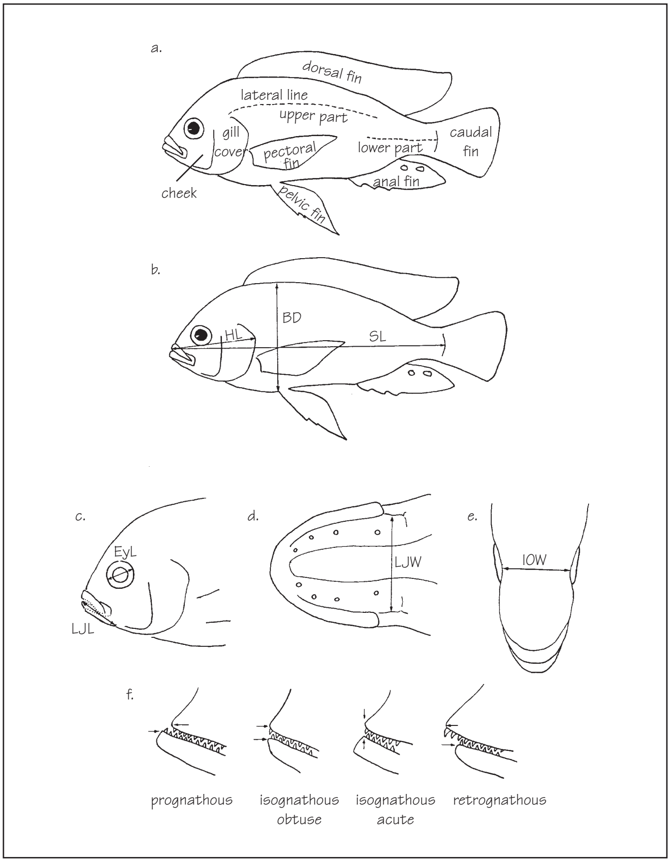
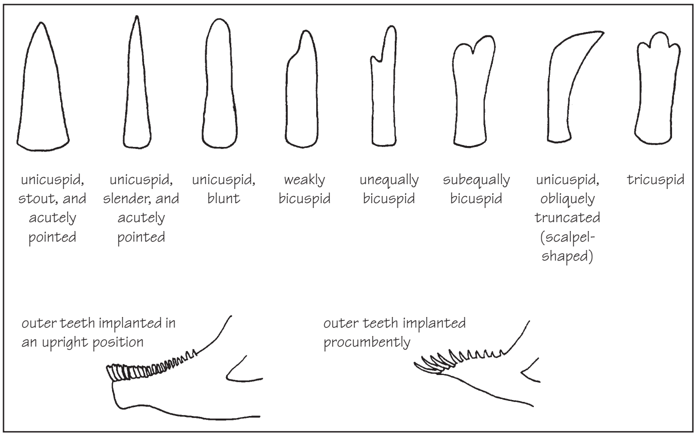


Figure 7. Morphological characters useful for identification of rock-dwelling haplochromines (parts d, e, f after Barel et al. 1977, altered).
a) Outline of a typical haplochromine cichlid with body parts relevant to species identification.
b) Standard length (SL), body depth (BD), and head length (HL).
c) Eye length (EyL) and lower jaw length (LJL)
d) Ventral view of the anterior head to show lower jaw width (LJW)
e) Dorsal view of the anterior head to show interorbital width (IOW)
f) Lateral snout outline.

Figure 8. Tooth shape and tooth implantation (after Barel et al. 1977, altered).
a) The most common shapes teeth in the outer tooth row.
b) Procumbent versus upright im-plantation of the teeth in the outer tooth row.



Chest squamation: generalized type (centre: *H. parvidens*-like) and rock-cichlid type (right: *H. cryptodon*; left: *H. melanopterus*).

should not be used as a means of assigning a sample of individuals to a taxonomic group, without reference to text and tables 3 and 4. Rather, it is meant as a guide to tentative identification of the taxonomic belonging of a species, which should then be checked against the diagnoses of species complexes, given in the text. Once the identity of a species has been traced down to the species complex, the species diagnoses in text and tables, in combination with the photographs hopefully allows identification to species level.

Furthermore it is important to note the following. The key is based on qualitative and quantitative measurements taken from about 800 male individuals of 125 species. Data from other publications (e.g. Greenwood) have not been considered. With a few exceptions, all measured fishes were within a size range of 70-100 % of the known maximum size of a species. Thus the key is neither suitable to identify subadults, nor adult females. Many haplochromine species undergo considerable changes in body shape during their life. Including subadult individuals in a key would mean to increase the intragroup variation that much, that a key would become entirely unworkable. Many haplochromine species, and rock cichlids in particular, exhibit strong sexual dimorphism. Females usually are smaller, often differ in head shape and dentition. Thus, considering females and males in one key would have an effect, similar to that of including subadults. It is possible to compile a separate key for females but I have not yet measured enough to do so. To begin with, I consider a key for males most useful because male coloration will in many cases help to confirm identifications and allow to identify a sample to species level after it has keyed out to one species complex.

Morphometric measurements were taken in agreement with the definitions given by Barel et al. 1977, and are shown in text figure 8. The same holds for the dental morphology (text figure 9). Abbreviations used in text, tables and identification key, are given in the text figures. Readers with a deeper interest in haplochromine alpha-taxonomy are strongly advised to read the work of Barel et al. (1977). With a few exceptions, only adults in a size range between 70 and 100 % of known maximum size of a species, and in most species only males, were measured for the data given in table 3. In the exceptional cases, males of the respective size had not been available. For measuring I used a digital calliper with glued-on divider needles, but normal divider and ruler do as well. Measurements are taken directly as the distance comprised between the points of the dividers placed on the measuring points (Greenwood 1956a, Barel et al. 1977). The number of vertical bars is generally counted between the pectoral fin, and the caudal end of the dorsal fin, and includes the bar that often starts dorsally ahead of the pectoral fin and, running slightly obliquely, passes across the pectoral fin insertion.

Key to (sub)genera and species complexes of rock-dwelling haplochromines

1. anal fin with 4 or more spines .... ***Astatoreochromis alluaudi***
   anal fin with 3 spines 2
2. 28-30 (maximum 32) lateral line pore scales .... ***Astatotilapia nubila***
   33 or more lateral line pore scales (32 in rare individuals) 3
3. Body depth < 27.5 % of SL; LJL <43 % of HL; lower jaw length/width ratio > 2.5; distinct mid lateral and dorsal lateral stripe present .... ***H (?)* "double stripe" complex**
   Body depth > 27.5 %, or otherwise different 4
4. LJL > 45 % of HL, if between 43 and 45 %, then LJL/W ratio > 1.7 and IOW < 22.1 % of HL .... ***Harpagochromis***
   LJL > 43 % of HL, if between 43 and 44 %, then LJL/W ratio < 1.7 or IOW > 22.1 % of HL 5
5. outer teeth in the LJ implanted procumbently, tooth band anteriorly in LJ describing a ventral inflection 6
   outer teeth in the LJ not procumbently implanted, tooth band not describing a ventral inflection 11
6. DHP decurved, outer teeth moderately to strongly (rarely only slightly) recurved, and unicuspid or weakly bicuspid; inner teeth small and arranged in broad bands anteriorly in both jaws or only in the upper jaw (one exception); IOW 24.0-27.8 % of HL (rarely only 23 %) .... ***Ptyochromis***
   DHP not decurved and/or dentition different and IOW < 24 % of HL 7
7. DHP shallow and straight; inner teeth tall, slender, implanted so as to lie almost horizontally, and deeply embedded in oral mucosa; head narrow, with an IOW from 21.1-23.8 % of HL (one case of 27.1 %); lower jaw usually narrow and attenuated .... ***Psammochromis***
   inner teeth not long and slender, not lying almost horizontally, and not deeply embedded in oral mucosa 8
8. HL less than, or equal to 33 % of SL (when 33 %, than EL > 24 % of HL) 9
   HL more than, or equal to 33 % of SL (when 33 %, than EL < 24 % of HL) 10
9. LJ shorter than, or equal to 34 % of HL (one exception); jaws isognathous or LJ shorter; mouth in most species lying horizontally; LJ and dental arcade narrow V- or narrow based U-shaped; DHP steep; chest scales small and deeply embedded ... **.... *Paralabidochromis* "rockpicker" complex**
   LJ longer than, or equal to 34 % of HL; jaws isognathous or lower jaw slightly longer; mouth lying obliquely; LJ and dental arcade not V-shaped, not narrow; DHP shallow to steep; chest scales neither small, nor deeply embedded ("short snout scraper" group) or small and deeply embedded and females bright yellow with black chessboard pattern ("rockkribensis") .. ***Paralabidochromis* "rockkribensis" complex**
10. Lips strongly swollen, often produced into lobes; prominent chessboard melanin pattern .... ***Paralabidochromis chilotes* complex**
    Lips not swollen to swollen but not produced into lobes; melanin pattern not prominent .... ***Paralabidochromis chromogynos* complex**

11. Large, protrusile mouth; either: outer teeth weakly bicuspid, short, in LJ inclined rostrad in some, deeply embedded in oral mucosa and often visible only after lips are pushed up, inner teeth so deeply embedded in oral mucosa that they are hardly visible; or: outer teeth longer, inner and outer teeth not very deeply embedded, but outer teeth in LJ inclined rostrad (1 species) .... ***Lipochromis***

    teeth neither deeply embedded in oral mucosa, nor inclined rostrad 12

12. Lower pharyngeal bone enlarged and stout, with enlarged, molariform pharyngeal teeth; oral teeth stout and unicuspid or weakly bicuspid .... ***Labrochromis***

    Lower pharyngeal jaw not enlarged and not with molariform teeth 13

13. Outer teeth bicuspid with a compressed major cusp that is laterally protracted and has a broad flange, or unicuspid and scalpel-shaped, strongly protracted, appearing obliquely truncated, moveably implanted .... ***Haplochromis***

    teeth different 14

14. DHP decurved; LJ short and broad, length/width ratio < 1.2; HL < 32.3 % of SL; teeth equally, subequally, and rarely unequally bicuspid, very closely set (usually contiguous); no or just a narrow gap between inner and outer teeth in the lower jaw .... ***Neochromis*** **I**

    DHP decurved or straight; length/width ratio of LJ > 1.2, if near 1.2, then teeth not contiguously set; inner teeth separated by a distinct gap from the outer teeth 15

15. BD < 32 % of SL .... ***Neochromis*** **II** (“unicuspid scraper”, “Bihiru scraper”)

    BD > 32 % of SL 16

16. HL < 32 % of SL, mid lateral stripe present that can be restricted to the area above the anal fin .... ***“Astatotilapia”*** **I** (*brownae)*

    HL > 32 % of SL, or no mid lateral stripe 17

17. outer teeth at least in adult males coarse, not moveably implanted, weakly bicuspid or unicuspid and crown recurved; interspaces between the teeth wider than the width of the tooth neck; DHP straight or incurved; EL < 27 % of HL 18

    outer teeth, also in adult males, moveably implanted; interspaces between the teeth narrower than the width of the tooth neck; tooth shape, DHP, and EL variable 19

    outer teeth strong, even in small fish not moveably implanted, unequally bicuspid and recurved; interspaces between the teeth narrower than the tooth neck .... ***“Astatotilapia”*** **II** (*barbarae,* “black long snout”)

18. IOW usually above 24 % of HL, if between 23 and 24 %, then both sexes with a prominent melanin pattern of 5-8 vertical bars on the flanks between the pectoral fin and the caudal end of the dorsal fin; in females generally 5-8 vertical bars .... ***H. (?) nyererei*** **complex**

    IOW below 24 % of HL; melanin pattern not prominent, consisting of 5-6 vertical bars on the flanks between the pectoral fin and the caudal end of the dorsal fin, if visible .... ***H. (?)*** **“deepwater” complex**

19. EL > 25 % of HL; IOW < 27 % of HL; HL <34 % of SL; mostly < 3 rows of inner teeth .... ***H. (?)*** **“pseudonigricans” complex**

    EL > 25 % of HL; IOW < 27 % of HL; HL >34 % of SL .... ***“Astatotilapia”*** **III** (“incurved dorsal head profile”)

    EL < 25 % of HL, if > 25%, then IOW >27% of HL and HL > 34% of SL, mostly > 3 rows of inner teeth, arranged in broad bands .. 20

20. outer teeth even in adult males unequally bicuspid .... ***Xystichromis*** **I**

    outer teeth in adult males unicuspid, coarse, and only slightly moveable; upright, crowns not recurved .... ***Xystichromis*** **II (“carp” complex)**

Introduction to the species discussions

On the following pages all cichlid species are discussed, that are currently known from rocky shores in south-eastern Lake Victoria. Nevertheless, it is likely that more, as yet unknown, rare or geographically restricted species live even within the part of the lake that we have surveyed. Additionally some species are discussed that are known from rocky places in other parts of the lake.

I have sorted the species into major groups and discuss them group by group. These groups will be referred to as (sub)-genera (see the chapter on taxonomy) if they were described as such by Greenwood (1980), or species complexes, if they are here described for the first time. The species account within each major group is preceded by a characterization of the group. Ranges of morphometric values that I give in these group characterizations are generally ranges among the mean values obtained from the different species that comprise a group. The resulting implications for identification purposes are discussed in the chapter on identification. To characterize groups that were defined by Greenwood (1980), I refer to his original definitions, and in cases, add information that I found to be of diagnostic value among the species I am discussing. To keep Greenwood's and my definitions apart, information cited or condensed from his descriptions is printed in italics. For the purpose of this book, I use from Greenwood's group diagnoses usually only characters that can be measured, counted, and observed on living fish.

Many of the species discussed on the following pages are undescribed and here discussed and introduced to a broader public for the first time. It should therefore be stressed that the data given in this book for various undescribed haplochromines do not constitute formal species descriptions. Undescribed species are given descriptive names, presented in quotation marks. These names have no taxonomic validity and do not conform to the rules of zoological nomenclature. Formal descriptions of a number of the here discussed species are under way. Descriptive names, when possible, were designed so as to provide two types of information about the "new" species: most apparent morphological characters (e.g. coloration) and information either about ecology or taxonomical position. In this way names like "yellow anal scraper" and "red head nyererei" denote a species that is an epilithic scraper with a yellow anal fin, and a *H. nyererei*-like species with a red head respectively. However, in cases where other descriptive names had already been used in previous publications, I keep to those, to avoid confusion.

Each species account includes information about coloration or other morphological characters that may help in identification. In this respect most species accounts are complemented by morphological information in two tables at the end of the book. In these tables mean values are given for a number of morphological characters that I found most helpful for identification purposes. In table 3 results of my measurements of most of the new and some described species are given. In table 4 the respective data are given, taken from previous publications, for a number of described species that occur at rocky shores, or are relevant to the identification of rock-dwelling species. More detailed information on these and other measurements will be given in forthcoming publications.

Each species account is complemented by a map, showing the geographical distribution of the species as currently known within south-eastern Lake Victoria. These maps are presented at the end of the book. Furthermore, each species account includes information on the ecology of the species, such as habitat demands, food, and behaviour if particulars are known. Morphologically and ecologically similar and/or closely related species, living sympatrically with the species under consideration, are mentioned in each species account. Further information is given optionally where it was considered relevant. The widely distributed matrix species (see the chapter on evolution) of the *Mbipi* species complexes are treated somewhat more extensively. Additional to the distribution maps more detailed maps are given on pages 17 and 65, showing Lake Victoria and the area surveyed for this book, with the most important places mentioned in the species accounts.

Angling for cichlids in rock holes.

Photographing *Haplochromis* in a cuvette at Zue Island.

Figure10: Lake Victoria and the area surveyed for this book with localities mentioned frequently in the text.

Vertical bar Mbipi

The haplochromine species joined in this group share a melanin pattern on the flanks that consists of four to eight dark vertical bars, that can in a few species occasionally be crossed by a faint mid lateral stripe. They are either narrow, numerous, regular in outline, and densely spaced, or broad, sometimes less regular in outline, and less many. All species have dark or bright male coloration.

Though adult individuals of the different species complexes within the vertical bar *Mbipi* can have very different tooth shapes, all have in common a rounded, not markedly narrowed dental arcade, and a more or less upright implantation of the outer teeth. Also those teeth anteriorly in the lower jaw are upright, rather than procumbent (figure 3 on page 30). The inner teeth are arranged in 2-7 (rarely 9) rows. In subadult individuals, the teeth in the outer row are usually moveably implanted. This condition prevails in lineages with bicuspid teeth in adults, whereas teeth become firmly attached in adults of lineages with coarse unicuspid teeth. All vertical bar *Mbipi* that we found in southern Lake Victoria have small to very small, deeply to very deeply embedded chest scales. Some species from Ugandan waters, however, have large, and not deeply embedded chest scales (see page 87ff). None of the known species has thickened lips.

Within the vertical bar *Mbipi*, five major lineages can be defined, that have different gross morphology. They overlap largely in the measurements of individual morphometric characters, but fall apart on combinations of different characters. The first of these lineages is characterized by a real rock scraper anatomy, reminiscent of *Pseudotropheus* in Lake Malawi, with a short head, usually strongly decurved dorsal head profile and broad jaws (*Neochromis*). A second one has similar scraper dentition, but has a longer head, straight dorsal head profile and less broad jaws (*Xystichromis*). Two lineages tend to have shallow dorsal head profiles, longer jaws, and get coarse unicuspid outer teeth when adult (*H. nyererei* complex, *H.* "deepwater" complex). The last lineage consists of anatomically quite unspecialized fishes with large eyes (*H.* "pseudonigricans" complex).

A melanin pattern like that of the vertical bar *Mbipi* occurs also in a few species that do not share other characters with this group, and do not live predominantly over rocks, e.g. species of the *Haplochromis* lineage, and *H.(?)* "thick skin".

Blue, black, and orange — the Neochromis complex of algae scrapers

By the time of Greenwood's last revision of the Lake Victoria haplochromines (Greenwood 1980), only one species of epilithic algae scrapers was known from this lake, *Haplochromis nigricans.* Two others were known from Lake Edward, *H. serridens* and *H. fuscus*. Greenwood placed them together into the resurrected genus *Neochromis* Regan, 1920. He defined this genus as *small haplochromines, with a very strongly decurved dorsal head profile (sloping at 70°-80° to the horizontal), a long, much coiled intestine (ca 3-4 times standard length of the fish), and broad bands of inner teeth anteriorly and anterolaterally in both jaws, not separated from the outer row. The outer teeth are equally or subequally bicuspid, their minor cusp is only a little smaller than the major cusp, their crown is compressed and broader than the body. They are very closely set (contiguous), moveably implanted, tall, slender but robust, showing only a slight antero-posterior decline in their height and size. The dentary (tooth carrying lower jaw bone) is markedly foreshortened, deep and stout, its anterior* *margin strongly curved medially so that the anterior outline of the lower jaw is almost rectangular. The lower jaw is with 30-38% of the head length short and broad, with a length/width ratio of 1.0 to 1.4.*

Greenwood suspected that there might be a second species of epilithic scrapers in Lake Victoria and this was confirmed in the late seventies, when two more species were discovered in the Mwanza Gulf area (van Oijen et al. 1981). Several further species were discovered only much later: in 1989 by myself in Uganda and in 1990 by N. Bouton in Tanzania. During our survey of rocky shores in the southeastern (Tanzanian) part of the lake, we discovered between 1991 and 1996 about 15 more species. Though their anatomical range exceeds in some characters (mostly in tooth shape and dorsal head profile inclination) the limits, set by Greenwood's definition of *Neochromis*, I am rather confident that these species, or most of them, constitute a monophyletic lineage to which I refer in the following as the *Neochromis* complex or *Neochromis* lineage.

I characterize the *Neochromis* complex by the combination of the following characters: Subequally to unequally bicuspid outer teeth (rarely weakly bicuspid outer teeth); 3 (rarely 2) to 7 (rarely 9) rows of inner teeth, arranged in broad bands anteriorly in the jaw, except in two species separated from the outer teeth by only a narrow gap or not separated at all; a lower jaw that tends to be square shaped and is on species average (with the exceptions of one morph of one species) not longer than 38% and not shorter than 33% of the head length and 0.9 to 1.2 (rarely 1.3) times as broad as long; a relatively short head (29.3-32.5% of SL); and 5 to 8 dark vertical bars on the flanks. Most species have a rather steep, decurved dorsal head profile, and all species from the southeastern lake have small, deeply embedded chest scales.

The species of the *Neochromis* complex are ecological equivalents to the species of the genera *Pseudotropheus* and *Tropheus* of Lakes Malawi and Tanganyika respectively. Their main food is epilithic *Aufwuchs*, the biocover of rocks, and in particular the algae component (Bouton et al. submitted). To obtain this food, a fish presses its slightly opened mouth against the rock and closes it, scraping with the teeth over the rock surface. Once filamentous *Aufwuchs* is held between the densely set teeth, the fish performs a jerking movement to tear it off. This so called "pull-scraping" is the main feeding technique of *Neochromis* species (Seehausen et al. in press [a]). However, other feeding techniques are applied and unicellular algae and various animal components of the *Aufwuchs* are eaten as well. Even plankton is frequently consumed (Bouton et al. submitted).

H. (Neochromis) nigricans (Boulenger 1906) is the only described *Neochromis* species in Lake Victoria. According to literature it is widely distributed in the lake and has been recorded from several places along the north coast, from an island in the central region as well as from Mwanza in the south (Greenwood 1956a, van Oijen et al. 1981). However, the taxonomic status of the different populations has to be investigated. My data suggest a disjunct distribution. In large parts of the area that we investigated, *H. (N.) nigricans* seems to be absent (see map). The measurements that I took from southern populations deviate slightly from Greenwood's data (Table 3 versus table 4), however, this may partly be due to personal differences in measuring. The species is characterized by a rather deep body, steep dorsal head profile, a very broad lower jaw, many rows of inner teeth, the outermost of which are hardly shorter than the outer teeth and by a male coloration that is rather uniform among populations: light blue with five to seven, in width and outline regular, darker grey to black vertical bars between the pectoral fins and the posterior end of the dorsal fin, a pale grey to reddish grey anal fin with very small egg dummies and a caudal fin that is usually entirely crimson. At some islands yellowish and very dark males occur sympatric with the normal coloured fishes. Females are usually yellowish brown with five to seven

Haplochromis (Neochromis) nigricans; male from Saa Nane Island.

H. nigricans; a territorial male in its natural environment.

H. nigricans; a male from an aquarium population.

A female *H. nigricans.*

A male *H. nigricans* from Igombe Island.

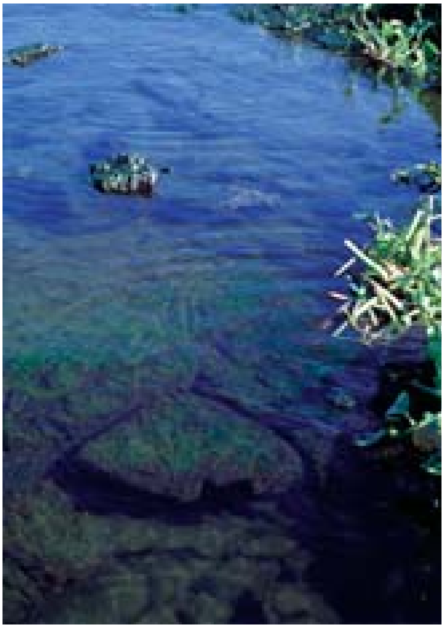
H. "black nigricans" from Chamagati.

H. "black nigricans", a freshly caught specimen.

A female *H*. "black nigricans"

An OB female *H*. "black nigricans"

dark vertical bars but in some populations exhibit a warm deep yellow that is particularly bright on the chin. The chest scales are small and deeply embedded. *H. (N.) nigricans* inhabits the shallow waters of most rocky areas within its geographical ranges but can be absent from large steeply sloping rocks and islands dominated by such rocks. Its highest densities are found between 1 and 2m water depth, depending much on the water transparency and thus the abundance of epilithic algae. In these depths it can be the



Chamagati Island

A female *H*. "yellow-blue nigricans"

dominant algae scraper. Males defend territories of usually more than a square metre surface on horizontal or gently sloping bottom. I frequently saw them chasing away also males of other *Neochromis* from their territories. Detailed stomach content analyses have shown that, though epilithic algae clearly dominate the food, its composition can vary considerably between seasons and geographical locations (Bouton et al. submitted). In periods of high abundance of other food organisms, e.g. plankton, insect larvae or prawns, *H. (N.) nigricans* can switch to these in spite of its specialized algae scraper morphology. In clear water areas filamentous green algae are eaten much more frequently than unicellular algae or filamentous blue-greens. However, the latter can form the major part of the diet in areas with murky waters like the central Mwanza Gulf. *H. (N.) nigricans* is absent from areas with very murky waters, e.g. the southern Mwanza Gulf.

***H. (Neochromis)* "black nigricans"** is a second species of "Nigricans-shape", and fits Greenwood's definition of *Neochromis*. It has a decurved dorsal head profile like *H. (N.) nigricans* and a similarly broad lower jaw. Its chest scales are small and deeply embedded. In contrast to the aforementioned species, *H. (N.)* "black nigricans" has entirely black males, that may have a narrow red edge on the caudal fin. In the latter case they closely resemble *H. (N.)* "velvet black" in coloration, and so do the females which are dark brownish. This species is known from very gently sloping islands with small and very small rock boulders in the Sengerema region west of Juma Island and from the steeper shores with bigger rock boulders of Juma Island itself. At Mafwinki Island it occurs sympatrically with a population of *H. (N.) nigricans*, at Juma Island with *H. (N.)* "Juma scraper", and at Chamagati Island it is the sole representative of the *Neochromis* algae scrapers but, like at the other places as well, coexists with the algae scraper *H. (Xystichromis)* "copper black" that occurs at most sampled locations outside the Mwanza Gulf. *H. (N.)* "black nigricans" is polymorphic, with an OB-morph, very similar to that of *H. (N.)* "velvet black" and *H. (N.)* "blue scraper", and with a piebald morph resembling that of *H. (N.)* "blue scraper" from Makobe and Gana Islands. The latter, however, is extraordinarily rare. Along the mainland shores between the islands west of Juma and the Mwanza Gulf, black *Neochromis* populations occur that are morphologically intermediate between *H. (N.)* "black nigricans" and *H. (N.)* "velvet black". I assume these species to be phylogenetically very closely related geographical vicariants. This notwithstanding, *H. (N.)* "black nigricans" is morphologically resembling *H. (N.) nigricans* much closer than *H. (N.)* "velvet black" (table 3). Ecologically it resembles *H. (N.) nigricans* and *H. (N.)* "blue scraper", living at 0.5 to at least 4 m water depth, and predominantly over horizontal to gently sloping surfaces. Of three individuals from Chamagati Island studied, two fed predominantly on algae (filamentous green algae and diatoms), one on caddis fly larvae, zooplankton and diatoms. The two that ate predominantly algae contained considerable amounts of mineral grains in the stomach, implying that they scrape the rocks with a powerful bite. We observed foraging fishes frequently moving in small shoals.

***H. (Neochromis)* "velvet black"**, discovered by E. Witte-Maas & F. Witte in 1979, is at many places among the most abundant *Mbipi*, particularly in the northern Mwanza Gulf. It is widely distributed and morphologically extremely variable. I consider all populations as belonging to one species because changes are gradual along geographical transects. *H. (N.)* "velvet black", or the "velvet black"/"black nigricans"/"blue scraper" superspecies, is known from almost each sampled rocky station and represents the matrix superspecies of the *Neochromis* lineage. A taxonomical description is under way, using populations from the northern Mwanza Gulf (Witte-Maas in prep.) which I therefore treat as the typical "velvet black". These populations are characterized by a dorsal head profile that is less strongly decurved than in *H. (N.) nigricans*, by subequally bicuspid to unequally and weakly bicuspid teeth in the outer rows (weakly bicuspid to unicuspid in large individuals), by maximum five and at least two inner rows, by male breeding coloration of uniform black with a narrow red caudal fin edge, by usually not more than five vertical stripes on the flanks between the pectoral fins and the posterior end of the dorsal fin, and by the occurrence of an OB morph, very similar to those of *H. (N.)* "black nigricans" and *H. (N.)* "blue scraper". Compared to *H. (N.) nigricans, H. (N.)* "velvet black" has a higher length/width ratio of the lower jaw, the inner tooth rows are (in most populations) separated from the outer row by a small gap and tricuspid outer teeth are a common feature laterally in the jaws but can even be found anterolaterally. The chest scales are small and deeply embedded.

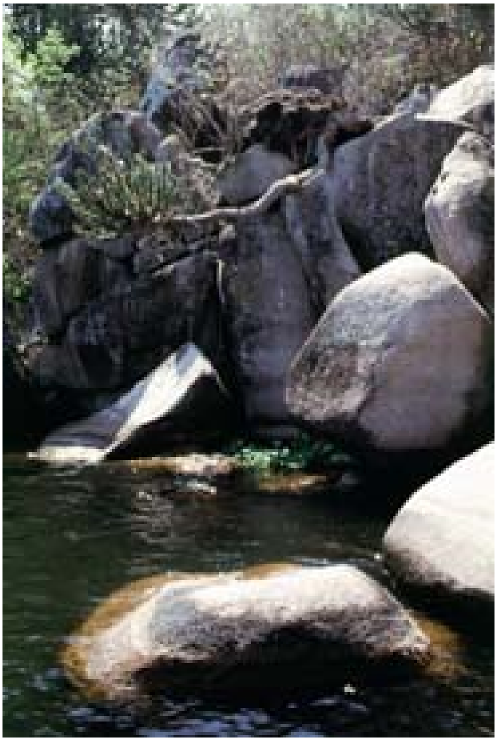
The distribution of such characterized populations extends from Hippo and Gabalema Islands in the North, via the Mwanza town area, Capri Point, Saa Nane, Ascari and Anchor Islands, to the Butimba and Nyegezi areas in the South. We consider this species to be much wider distributed, the populations, however, becoming increasingly different with increasing distance to the northern Mwanza Gulf. Along a transect from the northern Mwanza Gulf via the Gulf entrance to the exposed open mainland shores of the southwestern Speke Gulf, head shape and dentition gradually approach those of the more specialized algae scrapers *H. (N.) nigricans* and *H. (N.)* "blue scraper". The population at Igombe Island finally has even more and more narrowly spaced tooth rows (5-7 inner rows) than the sympatric population of *H. (N.) nigricans* (5-6 inner rows). All these populations share the above described coloration with the "Velvet black" from the northern Mwanza Gulf. They are usually found sympatric with *H. (N.) nigricans*, *H. (X.)* "copper black", and frequently with *H. (N.)* "giant scraper" and *H. (N.)* "unicuspid scraper". In contrast they have only exceptionally been found sympatric with *H. (N.)* "blue scraper" (see distribution maps). While the latter is known almost exclusively from islands in the open lake and western Speke Gulf, *H. (N.)* "velvet black" is in that region only known from the mainland shore. Populations from the shores of the central Speke Gulf resemble those from the northern Mwanza Gulf.

Populations south of the Nyegezi area in the Mwanza Gulf lack the OB morph, gradually change from the algae scraper morphology towards a more generalized morphology (with less decurved dorsal head profile, longer lower jaw, smaller minor cusp on the outer teeth and fewer inner tooth rows), and the deep black, typical of northern males, makes way for a coloration varying between grey-black, grey-blue and yellow-green. In the southern Mwanza Gulf greenish males with red chest are common. Along the same cline, the extension of red colour in caudal and anal fins is increasing. These southern populations are intermediate in dentition and coloration between the typical *H. (N.)* "velvet black" and the typical *H. (Xystichromis)* "copper black" which is absent from the Mwanza Gulf south of Python Island. The yellow-green morph resembles the southern most known population of *H. (X.)* "copper black" very closely in coloration. I do as yet not understand these patterns but it appears a possibility to me that *H. (N.)* "velvet black" and *H. (X.)* "copper black", while in the northern Mwanza Gulf and Speke Gulf representing two coexisting species, merge into a single polymorphic species in the southern Mwanza Gulf (see also the species *H. (?) nyererei* and *H. (?)* "zebra nyererei"). For a discussion of the apparent contradiction arising from the fact that the two species are assigned to two different subgenera, the reader is referred to pages 94. This is the only *Neochromis* algae scraper in the Mwanza Gulf south of Shadi area (*H. (N.) nigricans* has its southern most record at Shadi rocks).

Wherever *H. (N.)* "velvet black" coexists with *H. (N.) nigricans*, it has its maximum population density in slightly greater water depth than has *H. (N.) nigricans* and dominates over the latter around larger and more steeply sloping rock boulders. Ecologically it is thus similar to *H. (N.)* "blue scraper" that replaces *H. (N.)* "velvet black" at the offshore

A male *Haplochromis* "velvet black".

A female *H.* "velvet black".



The rocks at Hippo Island.

An OB male of *Haplochromis* "velvet black".

A territorial male *H.* "velvet black" from

An OB female of *H.* "velvet black".

islands in the open lake and western Speke Gulf. The diet of *H. (N.)* "velvet black" is very variable not only between populations but also between seasons. In the northern Mwanza Gulf this species is rather omnivorous, preying upon epilithic algae (predominantly diatoms but also filamentous algae), various epilithic fauna (Bryozoa, insect larvae, prawns), as well as on plankton and juvenile fish (Bouton et al. sub-

Below: an OB female *H.* "blue scraper".

mitted). At some islands moss animals (Bryozoa) are the dominant food item of *H.* "velvet black". The species lives in the northern Mwanza Gulf more cryptic (= hidden) than *H. (N.) nigricans*, males and brooding females defending rock holes and crevices as territories. However, in the southern Speke Gulf (Igombe Island) we observed adult males and females foraging in shoals, mixed with other species, at 2 to 3m water depth.

***H. (Neochromis)* "blue scraper"** is the third of three, over a large area complementally distributed species, that represent one superspecies (*H. (N.)* "velvet black", *H. (N.)* "black nigricans", *H. (N.)* "blue scraper"). It is known from all sampled offshore islands in the open lake and western Speke Gulf and from two less offshore localities (Ndurwa Point, Nansio/Ukerewe Island) that are inhabited by two, in coloration somewhat aberrant populations. The offshore "Blue scraper"-islands are separated from each other and from the mainland by 20 to 40m deep water and populations differ frequently in male coloration and body shape. At Makobe Island *H. (N.)* "blue scraper" is shallow bodied, the majority of the males are bright sky blue with rather widely spaced, weak vertical bars and red colour is completely absent from their fins. At Ruti Island *H. (N.)* "blue scraper" is very variable in male coloration. The majority of the males is also sky blue but somewhat darker than at Makobe Island, have darker vertical bars on the flanks, vivid red in the pelvic and anal fins and there are individuals with bright red caudal fins as well as individuals with completely black pelvics. Some individuals at Ruti Island are rather deep bodied. Males from the Mabibi Islands resemble the most common form of Ruti Island but the red in their pelvics is less vivid. Males of the deep bodied Bwiru Island population are dark in colours, with deep metallic blue flanks, and dark wine red anal and pelvic fins, those of Miandere Island are quite similar in coloration, but not so deep bodied, and at Gana Island they lack any red, like at Makobe Island but have darker and more narrowly spaced vertical bars. Also female coloration differs between populations. In some they are light yellowish with a bright yellow throat, in others they are more brownish with a grey throat. Interestingly we found rare brown female individuals also in populations with yellow females (e.g. Makobe Island), indicating that some of the interpopulation variation may have arisen via polymorphism.

All populations share an OB-morph very similar to those of *H. (N.)* "black nigricans" and *H. (N.)* "velvet black", the frequency of which is much higher at some islands than at others. Furthermore most, if not all populations have yellow males. Beyond that two other morphs are known from the Makobe Island population: piebald (shared with *H. (N.)* "black nigricans) and brassy and black, making it the most polymorphic of all known Lake Victoria cichlid populations. The black morph, though not entirely black, is rather similar to *H. (N.)* "velvet black" and *H. (N.)* "black nigricans" males, with a narrow red edge on the caudal fin. The piebald morph is also known from the population at Gana Island north of Ukerewe. Though hard data about the factors driving the evolution of the different male nuptial colour patterns in these isolated populations are lacking, circumstantial evidence suggests, that the coloration of other species that live sympatric with *H. (N.)* "blue scraper" may play a role. At Makobe Island, where *H. (N.)* "blue scraper" males lack dark vertical bars and red in their fins, the species coexists with *H. (N.) nigricans* whose males have dark vertical bars and a bright red caudal fin. Where the latter species is absent (Ruti, Mabibi, Bwiru, Miandere Islands), *H. (N.)* "blue scraper" males have dark vertical bars and red in their fins. At Gana Island again *H. (N.)* "blue scraper" lacks red in the fins, and it coexists with two other blue algae scrapers with extensive red in caudal and anal fins (*H. (N.)* "red tail giant scraper" and *H. (Xystichromis)* "red anal blue").

All populations of *H. (N.)* "blue scraper" have a specialized algae scraper dentition, very similar to that of *H. (N.) nigricans*, with densely set outer teeth, many inner tooth rows and no gap between outer and inner tooth rows. *H. (N.)* "blue scraper" lives at depths from 1 to 6m (Seehausen & Bouton 1996a), and inhabits steeply sloping large boulder as much as gently sloping small boulder shores. At the latter it overlaps largely with *H. (N.) nigricans* in depth but has its population density maximum in slightly greater depth than that species. Thus its spatial distribution is very similar to that of *H. (N.)* "velvet black". *H. (N.)* "blue scraper" feeds primarily on epilithic filamentous green and blue-green algae where it inhabits gentle slopes and on blue-greens and diatoms at steep slopes. Where it coexists with *H. (N.) nigricans* it eats relatively less green algae and more animal food than the latter but it consumes some insects everywhere (Bouton et al. submitted). Males at Makobe Island defend territories throughout the depth range down to 6m. While in the shallow water territorial males frequently interact with those of *H. (N.) nigricans* and *H. (X.)* "copper black", they interact with *H. nyererei* in deeper waters. Females and nonterritorial males are less gregarious than those of *H. (N.) nigricans*.

A population that is similar to *H. (N.)* "blue scraper" and *H. (N.) nigricans* in anatomy but does not agree with either of the two in coloration, lives at the Vesi archipelago in the Speke Gulf. The metallic deep blue flank coloration which is typical for *H. (N.)* "blue scraper", is replaced by a blue-grey, the ventral body outline is more convex than in that species, and the caudal fin is often red like in *H. (N.) nigricans*. However, the vertical bars are fewer (5-6) and less regular in outline, the lower jaw is longer than in *H. (N.) nigricans* and in contrast to the latter an OB morph exists, similar to those of *H. (N.)* "blue scraper" and *H. (N.)* "velvet black". Neither of these three more widely distributed species has been found in the Vesi archipelago. Since each other sampled station in the Speke Gulf is inhabited by a population of either *H. (N.)* "blue scraper" or *H. (N.)* "velvet black", it is likely that the fishes from the Vesi archipelago belong to this lineage and should then probably be regarded a population of *H. (N.)* "blue scraper". However, because of its peculiarities in coloration and body shape I consider ***H. (Neochromis)* "Vesi scraper"** distinct from "blue scraper" until more is known. In the Vesi archipelago it coexists in sympatry and parapatry with four other *Neochromis* but is usually more abundant than the four other species together. Alongside with *H. (N.)* "giant scraper", *H. (N.)* "short head nigricans", *H. (N.)* "eastern blue scraper", and *H. (Xystichromis)* "copper black" it inhabits gently, and moderately steeply sloping shores, and is absent from very steep islets that are inhabited by *H. (N.)* "yellow anal scraper". Its depth distribution ranges from the shallow water to at least 5 m.

***H. (Neochromis)* "Juma scraper"** is another poorly studied algae scraper that is similar, both, to *H. (N.) nigricans* and to *H. (N.)* "blue scraper" (Seehausen 1994). It differs from the first by a lack of extensive red coloration in the caudal fin, and by a longer lower jaw, from the latter by the absence of OB-morphs, and by a deeper body, and from both by a reddish anal fin. Males are either light blue or yellowish with 6 to 7 darker vertical bars on the flanks. Fully grown they become dark metallic blue-grey and exhibit a deep body with nuchal bump, while their dorsal head profile is not rounded as in most *H. (N.) nigricans* but remains rather straight, giving the fish a characteristic appearance. The red in the caudal fin is confined to a narrow rim. Females are brownish with yellow flush and a yellow throat. The species is known only from Juma Island, a big island with about 12 km of shoreline, in southern Lake Victoria. The possibility that *H. (N.)* "Juma scraper" represents a geographical form of *H. (N.)* "blue scraper" cannot yet be ruled out. However, considering the polychromatic character of *H. (N.)* "*blue scraper*" (OB morphs), *H. (N.)* "Juma scraper" may well be specifically distinct from it. It lives sympatrically with two other epilithic algae scrapers: *H. (N.)* "black nigricans" and *H. (X.)* "copper black". From both it is distinguished by male coloration (compare pictures) and by other morphology (table 3). It lives at depths down to 6m at least and at shores composed of large rock boulders as well as at places with me-

Haplochromis "blue scraper", piebald male.

An OB male *H.* "blue scraper".

A yellow male *H.* "blue scraper".

A black male *H.* "blue scraper"; below, a peppered female.

A blue male *H.* "blue scraper"; below a female.

The north-eastern part of the Vesi Archipelago in the Speke Gulf

A male H. "blue scraper" at Makobe Island.

A yellow male *H*. "blue scraper" at Makobe Island.

A male *H*. "Juma scraper".

A male *H*. "Vesi scraper"

A female *H*. "Vesi scraper".

An OB female *H*. "Vesi scraper"

dium sized boulders. More is not known about the ecology of this form.

***H. (Neochromis)* "yellow anal scraper"** is a species of "blue scraper"-like appearance, with an OB morph, whose specifically distinct status is apparent from its coloration and its coexistence with *H. (N.)* "blue scraper", *H. (N.)* "Vesi scraper", *H. (N.)* "eastern blue scraper" and *H. (N.)* "velvet black" at different localities. In contrast to these four species *H. (N.)* "yellow anal scraper" has a yellow to orange-red anal fin in the male sex, and a bright red caudal fin similar to that of *H. (N.) nigricans*. Male flank coloration is usually blue-green with many dark vertical bars, making a beautiful contrast to the bright yellow to orange anal fin. From *H. (N.) nigricans* and *H. (N.)* "blue scraper" it differs by a narrower tooth arcade, from *H. (N.) nigricans*, furthermore, in general appearance, anal fin coloration and a longer lower jaw. The species has a central/northern Speke Gulf distribution but within its range is largely absent from gently sloping shores. While very rare and rare at Ruti and Mabibi Islands respectively, where it coexists with *H. (N.)* "blue scraper", it is the only abundant *Neochromis* at steep islets in the Vesi archipelago and is absent from more gentle slopes which are occupied by four other *Neochromis* species. At Sozihe Islands, where *H. (N.)* "yellow anal scraper" coexists with *H. (N.)* "eastern blue scraper", *H. (N.)* "velvet black", *H. (N.)* "giant scraper" and *H. (X.)* "copper black", it is restricted to water depths beyond 4 m, and was found down to at least 7 m. *H. (N.)* "velvet black" seems restricted to immediately inshore shallow waters at moderately steep slopes, and *H. (N.)* "eastern blue scraper" to shallow waters at gently sloping places.

***H. (Neochromis)* "eastern blue scraper"** is another species of "blue scraper"-like appearance that, however, lacks an OB morph. From *H. (N.)* "blue scraper" it differs furthermore by a steeper, dorsal head profile (the head appears more round than in any other *Neochromis*), a somewhat shorter head, and by male nuptial coloration. Males are on the flanks dark blue, frequently appearing purplish blue when taken out of the water and their ca. 7 vertical bars are usually only faintly visible. Lips, snout and preorbital area are light blue. Females are usually brassy-yellowish.

We currently know *H. (N.)* "eastern blue scraper" from three islands in the east of our survey area. It lives at gently sloping to moderately steep rock shores, with small to medium sized boulders, and at water depths between 1 and 6 m. At Sozihe Island it is at relatively gentle slopes, at 1 to 3 m depth the most common haplochromine, numerically dominating over the sympatric algae scrapers *H. (N.)* "velvet black" and *H. (Xystichromis)* "copper black". It is at Sozihe Island also the only *Neochromis* species, that coexists with *H. (N.)* "yellow anal scraper" in depths beyond 4 m. At the very gently sloping small rock boulder and stone rubble shore of Zue Island "eastern blue scraper" is numerically codominant with the algae scrapers *H. (X.)* "copper black" and *H. (X.)* "short scraper". It seems to differ from the two others in depth distribution, being dominant at depths between 2 and 4 m, while the others are more abundant at 0.4 to 2 m depth. At Vesi Island "eastern blue scraper" is rare and coexists with the abundant *H. (N.)* "Vesi scraper" that seems to occupy a similar niche. *H. (N.)* "eastern blue scraper" is likely to be more widely distributed west of our survey area. It lives sympatric with many other *Neochromis* species: *H. (N.)* "Vesi scraper", *H. (N.)* "yellow anal scraper", *H. (N.)* "velvet black", *H. (N.)* "giant scraper" and *H. (N.)* "short head nigricans".

A species known only from the Vesi archipelago in the central Speke Gulf is ***H. (Neochromis)* "short head nigricans"**. Males are light blue with 6-7 darker vertical bars, a blue dorsal fin with red streaks and spots between the rays, a caudal fin that is distally red and proximally red streaked and a pale red anal fin with orange coloured egg dummies. Of all the epilithic algae scrapers studied by us, this one has on average the most extreme expression of equally bicuspid teeth in the outer row. Thus from a morphological point of view it is one of the most specialized epilithic algae scrapers.

"Short head nigricans" bears resemblance to *H. (N.) nigricans* and *H. (N.)* "giant scraper". From *H. (N.) nigricans* it is rather easily told apart on the ground of coloration and a shorter head, relative to the standard length. From sympatric *H. (N.)* "giant scraper" it differs most conspicuously by a steeper dorsal head profile, shorter lower jaw and more vivid red in the fins, particularly in the caudal fin. "Short head nigricans" seems not very abundant at Vesi Island. We found it only at one place, a moderately steeply sloping shore with medium sized rock boulders where it lives at about 4-5 m depth sympatric with *H. (N.)* "Vesi scraper", *H. (N.)* "giant scraper", *H. (N.)* "eastern blue scraper" and *H. (X.)* "copper black".

***H. (Neochromis)* "long black"** is one of several very slender and elongated *Neochromis* algae scrapers. Due to the elongated body shape, the dorsal head profile of these species is not as steep as in most other *Neochromis,* though it is decurved as well. In coloration *H. (N.)* "long black" resembles *H. (N.)* "velvet black", males being entirely black with red dorsal fin lappets. Different from *H. (N.)* "velvet black", however, the distal two thirds of the caudal fin are red and the anal is pinkish. We know this species from several localities around Ukerewe Island. All have relatively steeply sloping shores with medium sized to big rock boulders and most of them are surf exposed high energy shores. *H. (N.)* "long black" lives sympatric with the following other *Neochromis*: *H. (N.)* "velvet black", *H. (N.)* "blue scraper", *H. (N.)* "yellow anal scraper", *H. (N.)* "giant scraper", *H. (N.)* "red tail giant scraper", *H. (N.)* "black tail giant scraper" and with *H. (Xystichromis)* "copper black". It inhabits immediately inshore waters of less than 2m and slightly more offshore waters down to at least 7 m depth. We found it particularly abundant at Bwiru Island. Here some spatial niche segregation between "long black" and "blue scraper" can be observed with "blue scraper" numerically dominating in shallow waters, "long black" in depths beyond 5 m. Nothing more is known yet about its ecology. At Bwiru Island we collected one red male that may represent a rare colour morph of *H. (N.)* "long black".

***H. (Neochromis)* "Bihiru scraper"** presents a taxonomical and ecological puzzle. Known only from Bihiru Island at the western limit of the area surveyed by us, it may be more widely distributed west of that area. *H. (N.)* "Bihiru scraper" seems to be a trophically polymorphic species with an extraordinarily wide range of body shapes. One morph has a more typical algae scraper morphology with a shorter lower jaw (33.0-41% of head length), more inner tooth rows (table 3) and subequally bicuspid outer teeth that become unequally bicuspid only in fishes of more than 100 mm standard length, and are still weakly bicuspid in full adults of 135 mm standard length. Particularly smaller individuals of this morph have a relatively steep, decurved dorsal head profile. Individuals of the second morph have a rather straight dorsal head profile, irrespective of their size. Their lower jaw is longer (38.3-43.7% of head length), they have fewer inner tooth rows (table 3) and their outer teeth are weakly bicuspid already in fishes of 80 mm standard length, becoming unicuspid in individuals above 90mm standard length. There are two reasons why I consider these two forms to belong to a single species. (1) No consistent difference in male coloration exists between them. (2) The range of morphological variation exhibited by females is less wide and no two groups could be made.

Based on the same criteria, we consider *H. (N.)* "Bihiru scraper" specifically distinct from the sympatric population of *H. (N.)* "velvet black": Males of the first have usually a light red anal fin and a caudal fin that is red on at least the distal two thirds while those of the latter have a dark grey anal fin and a black caudal fin with narrow red edge. Morphological differences between the two species are among females as distinct as among males: *H. (N.)* "velvet black" (of the Bihiru population) have a steeper, more strongly decurved dorsal head profile, clearly more densely implanted teeth and no gap between outer and inner tooth rows (both morphs of "Bihiru scraper" exhibit

A male *H.* "yellow anal scraper".

A male *H.* "short head nigricans".

An OB female *H.* "yellow anal scraper".

A male *H.* "eastern blue scraper".

A male *H.* "long black" from Bwiru Island.

A female *H.* "eastern blue scraper".

A female *H.* "long black".

A red coloured male of Haplochromis "long black" from Bwiru Island.

The eastern shore of Bwiru Island, the natural habitat of H. "long black".

gaps). Furthermore does "velvet black" have the OB morph which is characteristic for many of its populations. However, more research, particularly on the ecology and on reproduction will have to show whether my current view is correct.

H. (N.) "Bihiru scraper" lives sympatric with two other *Neochromis* species, apart from "velvet black": *H. (N.)* "giant scraper" and *H. (N.)* "Labeo scraper", and also with *H. (Xystichromis)* "copper black". Big males of the bicuspid morph can be confused with "giant scraper" but differ by having the anal light red instead of dark grey with pink flush and by having fewer inner tooth rows (2 to 5 versus 4 to 8 in "giant scraper"). Big males of the unicuspid morph can be confused with unicuspid individuals of "copper black" (see below) which, however, have the red in the caudal fin restricted to a narrow edge. Males of *H. (N.)* "Bihiru scraper" undergo considerable changes in general appearance during ontogeny. Individuals of all sizes and shapes between 80 and 135mm standard length are found in breeding dress. Those of the bicuspid morph when below 100 mm standard length resemble *H. (N.)* "long black" but differ in coloration and

A male *H*. "Bihiru scraper", a bicuspid morph.

A male *H*. "Bihiru scraper", a unicuspid morph.

A female *H*. "Bihiru scraper".

have a higher lower jaw length/width ratio and fewer tooth rows, suggesting a lower level of specialization for algae scraping.

The shore of Bihiru Island slopes steeply to very steeply and has big to huge rock boulders. Within the available range, however, *H. (N.)* "Bihiru scraper" inhabits all microhabitats and depth ranges from less than 2 to at least 9 m depth. It is everywhere the most abundant algae scraper, and in part of its depth range, beyond 4 m, it is the only one.

It is not yet known whether an elongated *Neochromis* with a peculiar mouth, living sympatric with *H. (N.)* "Bihiru scraper" in shallow water at Bihiru Island, represents an extreme expression of the scraper morph of the latter or a separate species. This form has been named ***H. (Neochromis)* "Labeo scraper"** because of a strongly retrognathous lower jaw, resembling the mouth of the cyprinids of the genus *Labeo* and the Lake Malawi rock cichlids of the genus *Labeotropheus*. Its body is elongated like in "Bihiru scrapers" of similar size but the only obtained male is not black with a red anal fin but rather greenish-brown with a yellowish anal fin. It furthermore has bigger eyes than "Bihiru scrapers" of respective size. More individuals need to be collected before it will be possible to say whether it is specifically distinct from *H. (N.)* "Bihiru scraper".

***H. (N.)* "unicuspid scraper"** bears its name due to its dentition which, among the known epilithic algae scrapers, it shares only with the unicuspid morph of *H. (N.)* "Bihiru scraper". Small fishes still have typical algae scraper dentition with subequally bicuspid outer teeth but the outer teeth soon become weakly bicuspid and are in full adults usually unicuspid, widely spaced and moderately to strongly recurved. The inner teeth are arranged in 3 or 4 rows and are frequently also unicuspid and recurved. They are always separated from the outer teeth by a gap. Such dentition type was previously only known from snail eating cichlids that, with their teeth, pull the snail body out from the shell (Witte & van Oijen 1990; see the chapter on the *Ptyochromis* lineage). However, of the three individuals whose stomachs we analysed, none had eaten snails although snails were abundant in the environment (Igombe Island). Instead two ate predominantly filamentous blue-green algae and smaller amounts of filamentous green algae, and one had an empty stomach. All available evidence suggests that *H. (N.)* "unicuspid scraper" is an epilithic *Aufwuchs* eater.

In spite of its peculiar dentition *H. (N.)* "unicuspid scraper" is in general appearance and coloration very similar to *H. (N.)* "velvet black" and *H. (N.)* "blue scraper". Information about reproduction behaviour is needed before its specific status can finally be confirmed. This is particularly so because this species, at all its known localities, coexists in sympatry with either *H. (N.)* "velvet black" (Igombe Island, Bwiru Point) or *H. (N.)* "blue scraper" (Ndurwa Point, Makobe Island). At Igombe Island it is polymorphic for male nuptial coloration with black males, resembling *H. (N.)* "velvet black" and light blue males resembling *H. (N.)* "blue scraper". At the other places it is in coloration more grey-blue. Like "velvet black" and "blue scraper", it has also an OB morph. I think that *H. (N.)* "unicuspid scraper", *H. (N.)* "velvet black", and *H. (N.)* "blue scraper" form a complex of sibling species or that "unicuspid scraper" represents a trophic morph of one of them or even of both. The situation is very similar to that of the trophic morphs of *H. (N.)* "Bihiru scraper". However, the forms in the "velvet black"/"blue scraper"/"unicuspid scraper"-complex are further differentiated since the differences in head morphology and dentition are equally distinct in males and females, and are accompanied by some differences in microdistribution and male nuptial coloration.

H. (N.) "unicuspid scraper" lives at gentle to steep slopes and at places with medium sized to big rock boulders. Our data suggest that it differs in microdistribution from *H. (N.)* "velvet black": At Igombe Island the latter species inhabits depths from 0.5 to about 4 m, while "unicuspid scraper" lives between 2 and 6 m depth and can be observed at 6 m at the sand-rock interface.

Nevertheless, at intermediate depths we observed adult nonterritorial males of both forms in the same shoal. Other epilithic algae scraper species that live sympatric with "unicuspid scraper" are *H. (N.) nigricans*, *H. (N.)* "giant scraper" and *H. (X.)* "copper black".

***H. (Neochromis)* "giant scraper"** is the biggest member of the *Neochromis* complex (up to 150 mm standard length). It is rather widely distributed in the Speke Gulf, currently being known from the southern mainland shore between the entrance to the Mwanza Gulf and Senga Point, from most offshore islands in the western and central Speke Gulf and possibly from Ukerewe Island (one individual collected). Populations differ considerably in coloration with blueblack and black males at the mainland shores of Bwiru and Ndurwa and the inshore Igombe and Bihiru Islands, bright sky blue males at the offshore islands Makobe and Zue and more yellowish to grey-blue males at the other localities. The coloration of the population at Mabibi Islands is not yet known. The bright blue males of Makobe and Zue Islands resemble the most common morph of *H. (N.)* "blue scraper" at many islands (but not Makobe and Zue!) with red of variable extension and intensity in caudal and anal fins. The anal fin is pale to rather intensively red in blue males and is usually dark grey with a wine red to pinkish flush in dark males. The egg dummies are small and usually arranged in a single line. The caudal fin is proximally blue-grey with a faint red flush, distally reddish but never as intensely red as in *H. (N.) nigricans* or *H. (N.)* "yellow anal scraper". Females have a brassy sheen and yellowish fins that are particularly bright in the Zue Island population.

H. (N.) "giant scraper" has a characteristic head shape. The dorsal head profile is steep but rather straight, and the lower jaw slightly retrognathous and narrower than that of *H. (N.) nigricans* and *H. (N.)* "blue scraper". The mouth has a slight beaklike appearance. Even subadult individuals are readily recognized by their head shape. Intraspecific variation between populations exists in the steepness and curvature of the dorsal head profile. The species is rather variable in respect of the number of inner tooth rows and has, compared to *H. (N.) nigricans* and *H. (N.)* "blue scraper" more unequally than subequally bicuspid outer teeth.

H. (N.) "giant scraper" lives sympatrically with most other *Neochromis* algae scrapers: with *H. (N.) nigricans* and *H. (N.)* "velvet black" at many places, furthermore with *H. (N.)* "blue scraper", *H. (N.)* "eastern blue scraper", *H. (N.)* "yellow anal scraper", *H. (N.)* "unicuspid scraper", *H. (N.)* "short head nigricans", *H. (N.)* "Vesi scraper", *H. (N.)* "long black", *H. (N.)* "large eye nigricans", *H. (N.)* "pseudoblack" and with the *Xystichromis* algae scrapers *H. (X.)* "copper black" and *H. (X.)* "short scraper". The specific status of *H. (N.)* "giant scraper" is therefore certain. Nevertheless, we have found individuals, intermediate between this species and *H. (N.)* "velvet black", at one place at the southern Speke Gulf mainland shore.

From the Mwanza Gulf a *Neochromis* form was reported by Witte et al. (1992) under the name *H.* "kruising", that is said to have been intermediate between *H. (N.) nigricans* and *H. (N.)* "velvet black" ("kruising" = Dutch word for hybrid) but was characterized by a retrognathous lower jaw like "giant scraper". It went almost extinct after the Nile perch upsurge and, in spite of extensive search, only three individuals have been seen at three different places over the past five years: 1990 (Python Islands, N. Bouton pers. comm.), 1990 (Anchor Island, N. Bouton pers. comm.), 1995 (Nyegezi rocks). It is possible that ***H. (Neochromis)* "kruising"** is a geographical variant of *H. (N.)* "giant scraper" that seems to remain smaller than the Speke Gulf populations of the latter.

H. (N.) "giant scraper" is at gently sloping shores more abundant than at steeply sloping shores. The population from the Vesi archipelago for instance inhabits only the moderately steep slopes of the main island and is absent from some of the steeply sloping rock islets off the main island, the habitat of *H. (N.)* "yellow anal scraper". In the rather well studied communities of Makobe

A blue male *H.* "unicuspid scraper".

A black male *H.* "unicuspid scraper".

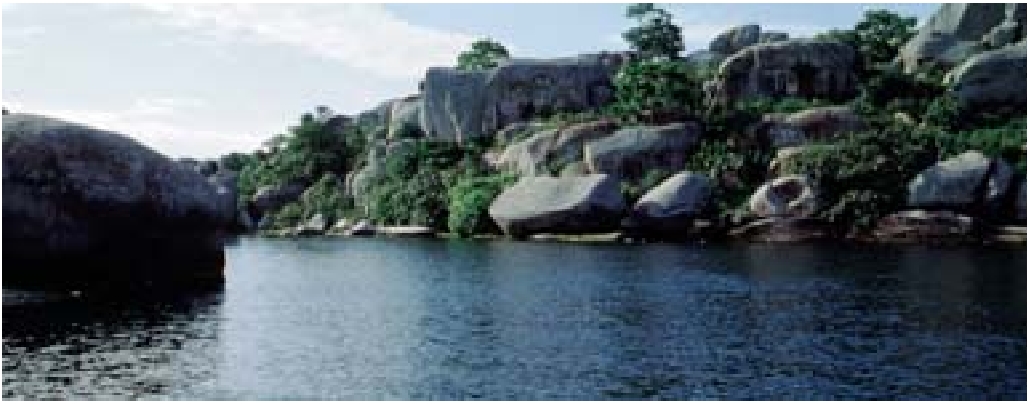
A female *H.* "unicuspid scraper".

An OB female *H.* "unicuspid scraper".

The only specimen known of *H.* "Labeo scraper" comes from Bihiru Island.

and Zue Islands, *H. (N.)* "giant scraper" is, among the *Neochromis* species, the one that has its maximum population density in the shallowest water. Adult males defend territories of several square metres, over rather horizontal bottom, at about 1 m water depth. Brooding females guard their fry in often not more than 0.5 m depth. However, the species is found down to 4 m depth. Nonbrooding fishes often move in shoals. *H. (N.)* "giant scraper" seems, among the *Neochromis* species studied, the most strict vegetarian. Of three individuals from Makobe Island, that we checked, one had eaten predominantly filamentous green algae, another one filamentous blue-green algae, and a third one higher plant material and diatoms. All three had eaten smaller amounts also of the other algae types while animalous food was hardly present in their stomachs (sometimes some chironomid larvae). It is almost impossible to catch "giant scrapers" with worm-baited hooks while most other *Neochromis* species readily take such baits. In the clear waters of Makobe Island we used to observe big males of this species paying no interest to, or even avoiding worm baited hooks, while other *Neochromis* (with similarly "specialized" algae scraper dentition) were quarrelling over them.

Only at Gana Island, the northern most of our sampling stations, we collected two other large *Neochromis* that differ from *H. (N.)* "giant scraper" in coloration



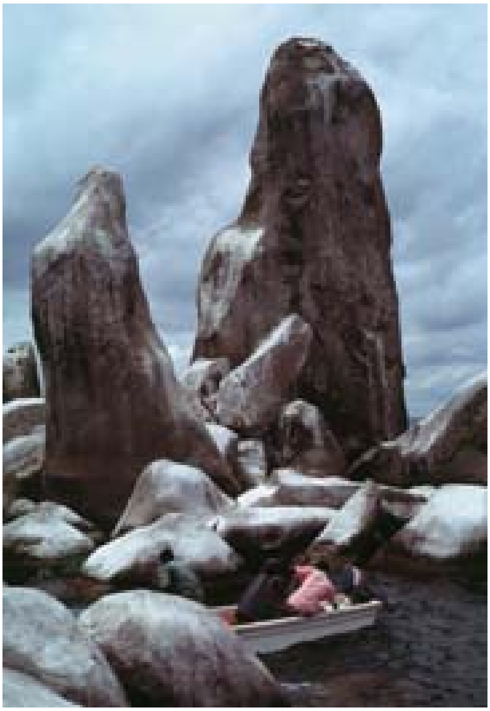
The north-western corner of Gana Island.

and mouth shape. It is likely that both, *H. (N.)* "red tail giant scraper" and *H. (N.)* "black tail giant scraper" have their major distribution outside of our sampling area. Males of ***H. (Neochromis)* "red tail giant scraper"** are blue with about six vertical bars, a caudal fin that is bright red in the distal half, a dark grey dorsal fin with red rim and red dots

A male *H*. "black giant scraper".

A male *H*. "giant scraper" caught in the net.

A male *H*. "giant scraper" from Makobe Island.



Filling up at Ruti Island.

between the rays and a silvery whitish anal fin with pink flush. They differ from those of the sympatric *H. (N.)* "blue scraper" population in coloration and body depth as well as by having a shorter and relatively broader lower jaw. From *H. (N.)* "black tail giant scraper" they differ in coloration and jaw shape (see below), from *H. (N.)* "giant scraper", that we did not find at Gana Island, by shorter but isognathous jaws, and male coloration. Closer resemblance exists between this species and *H. (N.)* "short head nigricans", currently thought to be endemic to the Vesi archipelago in the Speke Gulf. Too little is known about both populations, to interpret these resemblances.

***H. (Neochromis)* "black tail giant scraper"** is blueblack with about six vertical bars. All fins are black, the dorsal fin with some metallic blue in the hard part and red lappets, the caudal fins with a narrow red rim. Lips, snout and preorbital area are light blue. "Black tail giant scraper" is deeper bodied than the sympatric "blue scraper" population. A peculiar feature of this species is the shape of its lower jaw. It is V-shaped and at the tip slightly curved downwards, together with the slightly thickened upper lip creating a beak like appearance of the mouth.

The three morphologically similar *Neochromis* species that live sympatric at Gana Island, have distinctly different male anal fin coloration. "Red tail giant scraper" has, on a silvery whitish-pinkish fin, deep yellow egg dummies that are surrounded by a clear white inner ring and a transparent outer ring. "Blue scraper" has, on a grey anal with pale white edge, pale yellow egg dummies with only a transparent ring. "Black tail giant scraper" has dull yellow egg dummies on a black anal fin. These coloration differences may help females to recognize their males. *H. (N.)* "red tail giant scraper" and *H. (N.)* "black tail giant scraper" were caught, in the very clear water of Gana Island, at 4-5 m depth among big rock boulders.

One of the least known, and at the same time most peculiar *Neochromis* species is ***H. (Neochromis)* "large eye nigricans"** from Makobe Island. In spite of extensive collecting and ecological research at that island this species was caught only occasionally (3 individuals in 1992, 4 in 1993, none after that) and only in the female sex. This is the more peculiar, as in most other *Neochromis* species males are caught much more frequently than females. *H. (N.)* "large eye nigricans" resembles on the first glance *H. (N.) nigricans* but has a much narrower snout and lower jaw, a different dentition (the outer teeth are much longer and bigger than the inner teeth) and exceptionally big eyes (table 3). Either the species is extraordinarily rare or we have not yet detected its major habitat. Three individuals in 1993 have been caught at only 1 to 1.5 m depth, in a rock garden within a reef at the SW coast of Makobe Island, and one at less than 1 m depth at the edge of the reef. At the same spot *H. (N.) nigricans*, *H. (N.)* "blue scraper" and *H. (X.)* "copper black" are living. Of the three individuals caught in 1992 is only known that they were at less than 3 m water depth, together with *H. (N.)* "giant scraper" and the three above mentioned species. Recently some very similar individuals (again females) were collected at Nansio Island/ Ukerewe.

***H. (Neochromis ?)* "pseudoblack"** seems to stand rather isolated within the *Neochromis* complex if it really belongs here. It has a rather narrow head of a distinct shape and big eyes, resembling the species of the "Pseudonigricans" complex but with the strongly decurved and steeply sloping dorsal head profile of many *Neochromis*. The dentition of 3 individuals, collected in 1991 is typical for the latter group (subequally bicuspid outer teeth, 5-6 inner tooth rows). Four fishes, collected in 1993 and 1995 had only 3 inner rows and those two collected in 1996 only 2-3, while all had subequally bicuspid outer teeth. It is currently not possible to interpret these observations. In fishes below 85 mm standard length the lower jaw length/width ratio is higher than in typical *Neochromis* species but bigger individuals have a typical *Neochromis*-ratio of below 1.1. Males are dark brown-black with five to six vertical bands and an indication of orange sheen behind the pectoral fins. All unpaired fins are black with a narrow red margin. Females are light brownish and also carry five to six vertical bars on the flanks. *H. (N.)* "pseudoblack" partly resembles in coloration and general appearance *H.* "scraper pseudonigricans", a Pseudonigricans-group species with scraper morphology, though *H. (N.)* "pseudoblack" is morphologically a step further towards a specialized epilithic scraper. Nevertheless, phylogenetic affinities to the Pseudonigricans-complex cannot be excluded.

H. (N.) "pseudoblack" might be endemic to Ruti and Mabibi Islands in the centre of the western Speke Gulf and seems restricted to shallow (1-3 m depth) inshore places where it occurs in low densities among rock boulders, together with *H. (Xystichromis)* "copper black". We have not caught it in the slightly offshore areas beyond 2 m depth, the major habitat of *H. (N.)* "blue scraper".

The little data I have about *Neochromis*-like algae scrapers from the northern parts of Lake Victoria are mostly based on a short sampling trip to Jinja, done in 1989. The few they are, they do indicate two things: First, that the northern lake shores have a species-rich epilithic algae scraper community as well. Second, that there are some interesting differences between southern and northern *Neochromis*. I found five epilithic algae scrapers occurring sympatrically, three of which certainly belong to the *Neochromis*-lineage but we did not find fishes that match with Boulenger's (1906) description, and Greenwood's (1956a) redescription of *H. (N.) nigricans*. One species, ***H. (Neochromis)* "large scale nigricans"**, resembles the latter in coloration but differs from it in other morphological characters (Seehausen 1994): (1) Squamation of the chest. In *H. (N.) nigricans* (illustrated by Boulenger (1911) and redescribed by Witte & van Oijen (1990)) chest scales are small and deeply embedded. Several hundred specimens which I saw from the southern lake exhibit this feature that they share with all other southern *Neochromis*. In contrast, the fishes from the Napoleon Gulf in Uganda, show a generalized chest-squamation without scale size transition. As a consequence they have only four to six (mean 4.8) scales between the pelvic and the pectoral fin insertions, compared to 6-9 scales in Greenwood' s *H. (N.) nigricans*, and in the *H. (N.) nigricans* from the Mwanza area (mean 6.9). (2) The length/width ratio of the lower jaw is significantly higher in "large scale nigricans" than in *H. (N.) nigricans* from Mwanza (U test $p < 0.05$). (3) Oral jaw dentition: While *H. (N.) nigricans* as described by Boulenger, and our fishes from Mwanza have 5-7 rows of inner teeth in both jaws, "large scale nigricans" from Jinja has only 4-5. The difference between major and minor cusp of the outer jaw teeth is greater in "large scale nigricans", and teeth are more unequally than subequally bicuspid. Thus, in dentition *H. (N.)* "large scale nigricans" resembles some populations of *H. (N.)* "velvet black", rather than *H. (N.) nigricans* from the southern lake.

I cannot rule out the possibility that *H. (N.)* "large scale nigricans" will turn out to be conspecific with *H. (N.) nigricans* once more information will become available, particularly about the populations living along the shores between Jinja and the southeast. The dentition differences between *H. (N.)* "large scale nigricans" and, what I consider the typical *H. (N.) nigricans*, seem extreme for conspecific populations of rock-dwelling haplochromines. Nevertheless, the differences that we found among populations of *H. (N.)* "velvet black" within the Mwanza/ Speke Gulf area are of similar magnitude. Though the differences between *H. (N.)* "large scale nigricans" and *H. (N.) nigricans* are particularly striking because the intraspecific variability among southern

The rocky shore at Vesi Island.

A male *H.* "red tail giant scraper".

A female *H.* "large eye nigricans".

A male *H.* "black tail giant scraper".

A portrait of a male *H.* "pseudoblack".

populations of the latter is very little, dental morphology alone would therefore not be sufficient evidence for the specific status of *H. (N.)* "large scale nigricans". Stronger evidence may be the squamation differences.

Chest squamation has been considered such phylogenetically relevant a trait that Greenwood (1979) defined the haplochromine genus *Thoracochromis* (which does not occur in Lake Victoria) based on the single synapomorphy (shared derived character) of small and deeply embedded chest scales. The value of this trait for high level phylogenetic work has been questioned after it was found that most (southern) rock-dwelling haplochromines of Lake Victoria have *Thoracochromis*-like chest squamation (Seehausen 1994). However, no case is known to us in which conspecific populations of haplochromine cichlids would exhibit basically different patterns of chest squamation. Moreover, Boulenger (1911) depicts, as *Haplochromis simotes*, a typical small scaled *H. (N.) nigricans* from the Victoria Nile at Jinja. This implies that the small scaled species also occurs at Jinja. *H. simotes* was synonymised with *H. nigricans* by Regan (1922) because he considered the apparent difference in head shape between the holotype of *H. nigricans* and *H. simotes* an artefact of preservation in *H. nigricans*. To finally answer the question about the status of *H. (N.)* "large scale nigricans", *nigricans*-like populations from northern, eastern and western shores of the lake should be sampled, and the different populations be compared to the type material of *H. nigricans* and *H. simotes*.

***H. (Neochromis)* "slender scraper"** is a second *Neochromis* from Jinja (Seehausen 1994). In its elongated body shape and little decurved dorsal head profile it resembles *H. (N.)* "unicuspid scraper" and similar forms from the southern lake. From the sympatric *H. (N.)* "large scale nigricans" it differs also in dentition and squamation, having longer outer teeth and very small and deeply embedded scales in the chest and nuchal regions. In contrast to *H. (N.)* "unicuspid scraper" it bears in the outer row typical subequally bicuspid epilithic scraper teeth. The inner teeth are arranged in 6 to 8 broad bands. *H. (N.)* "slender scraper" lives sympatrically with two other *Neochromis*: *H. (N.)* "large scale nigricans", and *H. (N.)* "Jinja big

H. "slender scraper".

A male *H*. "pseudoblack".

A female *H*. "pseudoblack".

scraper", and with two other epilithic scrapers: *H. (X.)* cf. "copper black" and *H. (X.)* "Jinja blue scraper".

As ***H. (Neochromis)*** **"Jinja big scraper"** denoted is a bigger species from Jinja/Napoleon Gulf (Seehausen 1994) that resembles the sympatric *H. (N.)* "large scale nigricans" in its red caudal fin coloration, but has grey to blackish flanks, a less strongly decurved dorsal head profile, and a narrower lower jaw. Like those of *H. (N.)* "large scale nigricans", the outer teeth of *H. (N.)* "Jinja big scraper" are unequally to subequally bicuspid, and much longer than those of the inner rows. The only 4 to 5 scales between pectoral and pelvic fin are large and not deeply embedded. The species occurs sympatrically also with *H. (N.)* "slender scraper", *H. (X.)* cf. "copper black", and *H. (X)* "Uganda blue scraper".

From Entebbe/Uganda another species that is likely to belong to the *Neochromis* lineage was exported in the late 70s to Sweden by B. Selbrink as *H. (N.) nigricans* (Selbrink 1986). It turned out to be neither of the two by then known *Neochromis* species *nigricans* and "velvet black" and was given the name ***H. (Neochromis)*** **"cross dresser"** (L. Kaufman, pers. comm.). This is a somewhat elongate blueblack fish with red caudal fin. Very similar fishes have been exported from Kenya to Germany in the early 1990s by an aquarium fish exporter, and may still be in the aquarium fish trade. It is possible that several similar species are referred to under the name "cross dresser".

Yet another epilithic algae scraper species that resembles *H. (N.) nigricans* and likely came from Uganda or Kenya appeared in the 1980s in the aquarium trade under the name *Astatotilapia nubila.* I have suggested the working name ***H. (Neochromis)*** **"red anal nigricans"** (Seehausen 1994). Like several other northern *Neochromis* it has large, and not deeply embedded scales between pectoral and pelvic fin (I found 6 to 7 in very big fishes), but it differs from the others by having an entirely red anal fin in the male. Young adults have a less strongly decurved dorsal head profile than both, *H. (N.) nigricans* and *H. (N.)* "large scale nigricans".

Small and deeply embedded chest and nape scales have been interpreted as a derived character of phylogenetic value by Greenwood (1979) who described the genus *Thoracochromis* based on this character. Greenwood did not find species (or "possibly one") with deeply embedded chest and nape scales in Lake Victoria. In contrast van Oijen et al. (1981) had observed that many rock dwelling haplochromines in the Mwanza Gulf of Lake Victoria exhibit this feature, and argued that it might be an adaptation to life between rock boulders: large, loosely embedded scales are easily lost when fast escape swimming trough narrow gaps is required. Greenwood worked mainly at the northern lake coast, and of the four *Neochromis* species that I could examine from Uganda, only one had small, deeply embedded chest scales. In contrast, all of the species that I examined from the southeastern lake, between the Mwanza Gulf and Gana Island, had small, deeply embedded chest scales. Since many southern species also have broader lower jaws, more subequally bicuspid teeth, and more inner tooth rows (all characters associated with epilithic scraping) than northern species, it might be argued that they are adapted to different environmental conditions. Tank bred individuals of four populations of *H. (N.) nigricans* and several populations of other species from Mwanza and Speke Gulf, retained their squamation pattern over several generations. Thus, the type of chest squamation is certainly not merely a phenotypic response to different ecological conditions.

Xystichromis-like epilithic algae scrapers

Several of the above described species do not fall into Greenwood's narrow definition of the genus *Neochromis*, but with two exceptions share the among Lake

Victoria cichlids unique combination of a decurved dorsal head profile, a broad and short lower jaw, subequally bicuspid outer teeth and more than three inner tooth rows. One species (*H. (N.)* "unicuspid scraper") and one morph of a second species (*H. (N.)* "Bihiru scraper") have a shallow, and straight dorsal head profile, a longer and less broad lower jaw and unicuspid outer teeth. Nevertheless, I consider them *Neochromis* because in general appearance and relative head length, they closely resemble other species of that group, and at least one of them shares a colour polymorphism (black, blue, OB) with other *Neochromis* species. Several other species, though epilithic scrapers as well, deviate from *Neochromis* in relative head length, head shape, jaw and tooth shape and lack the OB-morph. With their straight dorsal head profile in spite of a deep body, with a longer head (species means >33% of head length with the exception of one species), a longer and less broad lower jaw (36.8-40.9% of head length, length/width ratio 1.30 to 1.49) and with usually more unequally than subequally bicuspid outer teeth, they match better Greenwood' s *Xystichromis*-, rather than his *Neochromis*-lineage.

Greenwood defined *Xystichromis* Greenwood 1980 as *small haplochromines with a long, much coiled intestine (ca. 3-4 times standard length), and broad bands (4-6 rows deep) of inner teeth anteriorly and anterolaterally in both jaws, narrowly , if at all separated from the outer row. The dorsal head profile slopes gently, and is not strongly decurved. The dentary (tooth carrying lower jaw bone) neither as deep and foreshortened as in* Neochromis*, nor as slender as in* Astatotilapia. *The teeth in the outer row of each jaw are very closely set, moveably implanted, tall, and slender but strong, showing only a slight antero-posterior decline in their height and size. They are unequally bicuspid, the minor cusp prominent but clearly smaller than the major one, the crown is not distinctly broader than the neck and body.* The head length of Greenwood's *Xystichromis* species ranges from 31.8 to 33.4% of standard length, the lower jaw length from 36.7 to 37.6% of the head length, and the length/width ratio of the lower jaw from 1.4 to 1.6.

Three species are currently described in *Xystichromis* Greenwood 1980. They were frequently considered epiphythic algae scrapers and plant eaters (Fryer & Iles 1972, Witte & van Oijen 1990), however, only for *H. (X.) phytophagus* Greenwood 1966, is the evidence unambiguous. Studied individuals had not only plant material in the stomachs but were in fact caught over sand bottom near rooted vegetation (Greenwood 1966). Respective habitat notes are not available for *H. (X.) bayoni* (Blgr.) 1911 that was collected from the Victoria Nile, connecting Lakes Victoria and Kyoga (Greenwood 1960). *H. (X.) nuchisquamulatus* (Hilgend.) 1988 was collected from exposed littoral zones in Lake Victoria and even from the far offshore Godziba Island in the centre of the lake (Greenwood 1956a). Stomach contents, analysed by Greenwood (1960), were composed of fragments of plant tissue and numerous filamentous algae that Greenwood calls "epiphytic" without giving evidence for their actual growing on plants rather than on rocks. He mentions *Oedogonium* which we frequently find in the stomachs of epilithic algae scrapers and Greenwood's habitat notes for *H. (X.) nuchisquamulatus*, particularly its occurrence at the isolated rocky Godziba Island, suggest to me, that this species might be an epilithic scraper.

***H. (Xystichromis)* "copper black"** is the most widely distributed of all known epilithic algae scraper species, and the matrix species of the *Xystichromis*-lineage. We found it at almost every rock shore and rocky island except in the southern Mwanza Gulf, south of Python Island and at the very steep slopes of some islands in the northeastern Mwanza Gulf. A population that might be *H. (X.)* "copper black" has also been found near Jinja at the

A male *H*. "red anal nigricans".

A territorial male *H.* "copper black" at Chamagati Island

A territorial male *H.* "copper black" at Makobe Island northernmost end of the lake (A. Meyer pers. comm., pers. obs.). This is also ecologically probably the most versatile of all known epilithic algae scrapers, if not of all *Mbipi*. It inhabits various stony and rocky habitats, including stone-sand mixed substrates. It is, however, absent from some very steeply sloping rocky islands and mainland shores and is generally more abundant at gently sloping shores, with small and medium sized boulders. At many such places it is the numerically dominant cichlid species, living between 0 and 6 m water depth with the maximum density between 0 and 2 m depth (Seehausen & Bouton in press). The well studied population from Makobe Island feeds on a variety of food items such as diatoms, filamentous epilithic algae, detritus, insect larvae and moss animals (Bryozoa) and is more appropriately described as an epilithic omnivore than as an algae scraper (Bouton et al. submitted). In this respect it is similar to the *H. (N.)* "velvet black" populations of the Mwanza Gulf. Like in *H. (X.) nuchisquamulatus*, fragments of rooted plants are usually found in the stomachs of *H. (X.)* "copper black". From Scuba observations at Makobe Island we know that they are usually taken in as detritus, sedimenting among the rocks and are usually not browsed off living vegetation. Similar feeding be-


A male *H*. "copper black" from Makobe Island.


A female *H*. "copper black" from Ruti island.


A female *H*. "copper black".


Amranda Point; small boulders are typically found in the habitat of *H.* "copper black".

haviour could account also for the presence of plant material in *H. (X.) nuchisquamulatus* stomachs.

Unfortunately live coloration of *H. (X.) nuchisquamulatus* is not known. However, *H. (X.)* "copper black" differs from the latter and from the other described *Xystichromis* species in other morphological features, i.e. has a smaller lower jaw length/width ratio and a distinctly smaller eye diameter (compare table 3 with table 4). In terms of coloration many populations of *H. (X.)* "copper black" are similar to *H. (Neochromis)* "velvet black", from which they differ mainly in having a wine-red anal fin rather than a black one with a red rim. The black males of "copper black" usually exhibit a coppery sheen on the cheeks and sometimes on the flanks which we have never seen in *H. (N.)* "velvet black". In some populations of *H. (X.)* "copper black" males are yellow-green rather than black, in others they have blue lips.

The relationship between *H. (Xystichromis)* "copper black" and *H. (Neochromis)* "velvet black" is one of the many taxonomical puzzles among the rock haplochromines. Prior to our extensive rock shore survey *H. (X.)* "copper black" and *H. (N.)* "velvet black" were regarded as one species (see for instance Seehausen 1994 who used the term *H.* "velvet black Speke Gulf" for *H. (X.)* "copper black"). However, morphological and ecological data collected in the meantime show that these are two species that coexist in sympatry in large parts of their geographical ranges. *H. (X.)* "copper black" differs from *H. (N.)* "velvet black" not only in male coloration but also in head shape and dentition. The first one has a less decurved, rather straight dorsal head profile and the outer teeth are less closely spaced and often more unequally, rather than subequally bicuspid than in most (not all) populations of *H. (N.)* "velvet black". Where the two species coexist, males of *H. (X.)* "copper black" are often more yellow-green than black (e.g. Python Island), while they are black at places from which *H. (N.)* "velvet black" is absent (e.g. Makobe Island). The colour difference between breeding males of the two species remains distinct even after preservation. A further striking difference between the two species is that *H. (X.)* "copper black" lacks the OB morph which is so characteristic of all, except the southern Mwanza Gulf populations of *H. (N.)* "velvet black" and of several other *Neochromis*: black blotches on orange to pink ground. Instead *H. (X.)* "copper black" has an extremely rare OB-like morph that carries some orange blotches on a black or brown body. Among the several thousand individuals that we have seen of *H. (X.)* "copper black" were only two individuals of this morph that may be produced by recurrent mutation. Both individuals were males. Where *H. (X.)* "copper black" and *H. (N.)* "velvet black" coexist, the first often tends to dominate in shallower and more inshore reaches, the latter in deeper and more offshore water or at steeper slopes. *H. (X.)* "copper black" occurs sympatrically with all *Neochromis* and both below described *Xystichromis* algae scrapers.

My grouping of "copper black" and "velvet black" into two different subgenera of algae scraping haplochromines seems to contradict the close similarity observed between certain populations of them. This is due to unusually extreme intraspecific variation among populations of "velvet black". While "copper black" matches better Greenwood's *Xystichromis* than his *Neochromis* lineage (Greenwood 1980), and many populations of "velvet black" match Greenwood's *Neochromis* lineage, others deviate from the latter into the direction of *Xystichromis*, while maintaining a typical "velvet black" appearance. Greenwood already arrived at the conclusion that *Xystichromis* and *Neochromis* are closely related sister groups within one superlineage (Greenwood 1981). It is therefore not surprising to find closely resembling species in both groups or bridging between the groups. If their resemblance indeed reflects particularly close phylogenetic relationship, the separation of the lineages *Neochromis* and *Xystichromis* may have to be revised.

A second deep bodied epilithic algae

scraper with a straight dorsal head profile is the small ***H. (Xystichromis)*** **"short scraper"** that is known only from Zue Island, near the northern shore of the central Speke Gulf, but may be distributed more widely east of the surveyed region. This fish, though on first glance easily confused with *H. (X.)* "copper black", is of a characteristic appearance. Relative to its large head, its body is short, giving it a heavy headed appearance. The upper lip of males is distinctly swollen and the premaxilla rather bullate. Males occur in two colour morphs: one green-blue, the other one yellowish. In contrast to *H. (X.)* "copper black", this species does not exhibit any red in its fins. Females are often very dark, almost blackish brown. Little is known about the ecology of *H. (X.)* "short scraper". It inhabits the very gently sloping small boulder shore of Zue Island from the surf zone to at least 4.5 m depth. In some very shallow places it can be the numerically dominant cichlid species, occurring in very high population density. At other places *H. (X.)* "copper black is more abundant and again at others *H. (Neochromis)* "eastern blue scraper". A third epilithic scraper, living sympatric with "short scraper", is *H. (N.)* "giant scraper". The dark, brown-black colour of "short scraper" females suggests that also females are frequently territorial.

H. (Xystichromis) **"red anal blue"** is a little known species that we recently discovered at Gana Island northwest of Ukerewe, the northern most point in our survey. In body shape it is very similar to *H. (X.)* "copper black" though its head is somewhat shorter relative to its standard length and its lower jaw shorter relative to its head length (table 3). In these measurements it is close to *Neochromis* but it has the straight dorsal head profile typical for *Xystichromis* and a *Xystichromis*-like dentition with unequally rather than subequally bicuspid teeth in the outer row. This is a brightly coloured species with two male colour morphs. One is light blue, the other one yellowish. Both have a bright orange-red anal fin with orange coloured egg dummies, and a caudal fin that is similarly bright orange-red in its lower half, and grey with red streaks and a red rim in the upper half. At Gana Island this is the only *Xystichromis*-like rock scraper that we found but it coexists with at least four *Neochromis* and two *Paralabidochromis* rock scrapers. Its habitat consists of large to huge rock boulders that form extensive rock gardens with steep walls as well as sun exposed vertical surfaces with algae cover. We found *H. (X.)* "red anal blue" at water depths from 3 to at least 5 m, where it was one of three abundant rock scrapers, *H. (Neochromis)* "blue scraper" and *H. (Paralabidochromis)* "yellow anal picker" being the other two. Possibly *H. (X.)* "red anal blue" is north of our survey area more widely distributed.

Similar to *H. (X.)* "red anal blue" is a species that is known only from the northern, Ugandan lake shore. It had been imported to Sweden by B. Selbrink under the name *Psammochromis riponianus* (Selbrink 1985). Probably the same species has more recently been collected again at Jinja/Uganda by A. Meyer (pers. comm., pers. obs.). I had suggested the descriptive name "Uganda blue scraper" for it (Seehausen 1994). Males of ***H. (Xystichromis)*** **"Uganda blue scraper"** are bright blue with red in all unpaired fins and 6-7 vertical bars on the flanks. Both sexes have quite long subequally bicuspid outer teeth and 3-4 inner rows. Nice photographs were published in the Swedish journal "Akvariet" (Selbrink 1985). The species lives sympatrically with *H. (X.)* "copper black" and *(N.)* "large scale nigricans" at Jinja.

H. (Xystichromis) **"large eye black"** is known from only a few individuals, caught at Igombe Island in the southern Speke Gulf. This species resembles *H. (X.)* "copper black" and *H. (N.)* "velvet black" in coloration but differs from both in the anatomy of the jaws (longer and less broad lower jaw), in dentition (less closely set outer teeth, fewer inner rows) and most strikingly by its larger eyes. The eye size of "large eye black", unlike eye sizes of the four above discussed species, matches that of the three described *Xystichromis* species. Males of *H. (X.)* "large eye black" are entirely black with an anal fin that is bright red in

A male *H.* "short scraper" from Zue Island.

A female *H.* "short scraper".

A male *H.* "large eye black" from Igombe Island.

A female *H.* "large eye black".

A male *H.* "red anal blue" from Gana Island.

A female *H.* "red anal blue".

its distal half, and with a red caudal fin edge. The dorsal head profile resembles that of *H. (X.)* "copper black" but is slightly more decurved and not concave. At Igombe Island *H. (X.)* "large eye black" coexists with *H. (Xystichromis)* "copper black" and with several *Neochromis* algae scrapers: *H. (N.) nigricans*, *H. (N.)* "velvet black", *H. (N.)* "giant scraper", *H. (N.)* "unicuspid scraper". The only epilithic algae scraper population with similarly large eyes is *H. (N.)* "large eye nigricans" from Makobe Island. Like that one, also *H. (X.)* "large eye black" has been collected in shallow immediately inshore waters (1-2 m depth) among rock boulders and in rockpools but not in deeper parts of the habitat, as opposed to what could have been expected from the large eyes. The two species, however, differ considerably in head shape and dentition. Nothing is known about the feeding habits of *H. (X.)* "large eye black".

The "carp" complex of big *Xystichromis*-like algae scrapers

The species of this species complex share the following morphological features: large to very large size with a relatively long (species means 32.0-32.7% of standard length) and broad head, a lower jaw that is longer than in *Neochromis* complex species (38.1-40.7% of head length), a dorsal head profile that is straight or slightly concave, and a dentition that differs from all dentition types previously known from Lake Victoria cichlids: unequally bicuspid to blunt, sometimes slightly recurved, unicuspid (big fishes) teeth in the outer tooth row and many inner rows that form

Fishermen at Makobe Island

A territorial male *H*. "carp" in the aquarium.

broad tooth bands, like in the other algae scrapers, but are separated from the outer row by a well developed gap. Small individuals have, like other epilithic algae scrapers, subequally bicuspid teeth in the outer row. None of the species of the *H.* "carp" complex is described and thus this group was not considered in Greenwood's revision of 1980. My morphometric measurements fall into the range of described *Xystichromis* species, with which "carp" complex species also share the straight dorsal head profile and the broad bands of inner teeth. In spite of their deviation from described *Xystichromis* in terms of outer tooth shape, I assign the species of this complex to Greenwood's *Xystichromis*-lineage until a revision of the algae scraping Lake Victoria haplochromines clarifies their position.

Most members of the "carp" complex live at gently sloping to moderately steep shores. Our stomach contents analyses of several species suggest that they are real filamentous algae scrapers, in spite of the outer tooth shape and rather wide setting which appear unsuitable for the loosening of firmly attached filaments. Laboratory experiments with *Haplochromis* "carp" had shown earlier that this species feeds by scraping and snapping (Seehausen 1994). All species seem to have a geographically rather narrowly restricted distribution and, with one exception, all are allopatric.

***Haplochromis (Xystichromis)* "carp"** was the first species discovered in this species complex. N. Bouton first collected some individuals in 1991 at Makobe Island in the Speke Gulf (Seehausen 1994). *H.* "carp" is one of the few bright yellow *Mbipi*. On the lemon yellow flanks males carry 5 to 6 black vertical bars. The caudal fin is reddish, the anal fin bright sky blue with a broad red edge, the dorsal fin in the spinous part metallic sky blue, in the soft part more hyaline with numerous bright red streaks and dots. There are usually two or three broad black blotches on the dorsal fin basis. Females are light yellowish brown. Discovered at Makobe Island, we know the species meanwhile also from Mponze Point, from which Makobe Island is separated by 5 km of more than 20m deep water, from Ndurwa Point, from Bwiru Island off the southwestern corner of Ukerewe Island and from Chamagati and Matwinki Islands in the Sengerema region. It seems thus a relatively widely distributed, though often rare species. Male coloration varies little among and within populations, but variation in other morphological characters such as dentition is sometimes that pronounced within populations, that one could think of different species.

H. (X.) "carp" inhabits exclusively the shallow reaches (0 to 2 m depth) of gently sloping small rock boulder shores, in particular somewhat surf protected microhabitats like little bays. We observed big territorial males in only 0.5 m water depth under floating roots of reed mats. *H.* "carp" is a solitary and rather cryptically living species that occurs in low population density. Of three individuals of which we studied stomach contents, two had eaten almost exclusively filamentous green algae, the other one filamentous blue-green algae. All had also ingested small amounts of plant (phanerogam) tissue and two had eaten a few insect larvae.

Close to *H. (X.)* "carp" is ***Haplochromis (Xystichromis)* "orange carp"** which is known only from Zue Island, near the northern shore of the central Speke Gulf. From *H.* "carp", this species differs in melanin pattern and male coloration. It has more (7 to 9) and more closely spaced vertical bars on the flanks. Males exhibit a warm orange coloration on the flanks and a reddish anal fin instead of the blue anal fin with red edge of *H.* "carp". Like *H (X.)* "carp" at other localities, does also *H.* "orange carp" inhabit at Zue Island the very shallow water. Between 0.4 and 1 m depth it is more abundant than *H. (X.)* "carp" is at other islands. However, "orange carp" seems even more narrowly restricted in its depth distribution. Among many hundreds of cichlids that we collected in nets set at depths between 1 and 5 m at Zue Island was only one "orange carp", caught in 1.2 m depth.

***Haplochromis (Xystichromis)* "red carp"** is one of three known bright red epilithic algae scrapers (the others are *H. (Paralabidochromis)* "rock macula" and *H. (P.)* "red short snout scraper"). Young individuals are morphologically rather similar to *H. (X.)* "carp" and *H. (X.)* "orange carp". Adults have a shorter lower jaw and very different coloration. Males have operculum and the lower half of the flanks bright red to pinkish red. The upper half of the flanks is grey with a reddish sheen but occasionally the entire flanks are red. The head is greyish, lips and cheek usually light blue. The anal fin is red with orange coloured egg dummies, the caudal fin is reddish with a deep red edge, the dorsal blueish grey with red lappets and red dots in the soft part. The pelvic fins are half black and half red. *H. (X.)* "red carp" is known only from two localities, about 30 km apart from each other, along the western shore of the Mwanza Gulf. It may be more widely distributed along that shore, although we did not find it at three collecting localities between the two places. The two populations differ in coloration (the kind of red, see photos) and at least in one morphometric value, suggesting that they are geographically isolated from each other. The population from Buyago rocks (southwestern Mwanza Gulf: Smith Sound, *H.* "pink giant" in Seehausen 1994) has a significantly smaller lower jaw length/width ratio. Furthermore it has a steeper dorsal head profile than the population from Kissenda Island (northwestern Mwanza Gulf).

Buyago rocks are of a rather rare kind of rock habitat: large, almost unbroken slabs slope gently down from *Euphorbia* forest covered hills to the shallow bottom of the Smith Sound. Below the water surface the slabs are eroded into rock boulders of 30 to 60 cm diameter. These boulders form pure rocky substrate only down to a water depth of 1-1.2 m, followed by rock/sand mixed substrate or rocks, covered with a layer of sand. *H. (X.)* "red carp" lives here at 0.5 to at least 2 m water depth and is the most abundant haplochromine species after *H. (Neochromis)* cf. "velvet black". Like the latter it inhabits the pure rock, as well as the rock/sand mixed substrates. Of three studied individuals, one had an empty stomach. One had been feeding predominantly on filamentous blue-green algae, as well as on some filamentous green algae. The third one had been feeding to about equal parts on moss animals (Bryozoa), may fly (Ephemeroptera) larvae and filamentous blue-greens.

Kissenda Island consists of medium sized rock boulders and slopes rather gently to moderately steep. Algae scrapers are not very abundant at this island. *H. (Neochromis)* cf. "velvet black", *H. (N.) nigricans* and an unidentified species of the *H. (Paralabidochromis)* "short snout scraper" complex, coexist with *H. (X.)* "red carp". The latter is numerically the dominant one and lives between 1 and at least 4, possibly 6 m depth. Though morphologically a scraper, the only individual of which we checked the stomach had eaten almost exclusively chironomid larvae. It is noteworthy that this species coexists at Kissenda Island with a second very big and entirely red *Haplochromis*: *H. (Ptyochromis)* "red giant sheller" (see page 200)

At Bwiru Island off the southwest corner of Ukerewe Island we collected a male of a "carp"-group species that in coloration resembles *H. (X.)* "red carp" but differs in dentition. At a size (104.9 mm SL), at which the latter has weakly bicuspid teeth in the outer row, it has still sub- to unequally bicuspid teeth. Until more individuals become available we treat the Bwiru Island population as ***H. (Xystichromis)* cf. "red carp"**. Interestingly it lives sympatric with *H. (X.)* "carp" which seems to have the normal "carp"-group tooth shape but has unusually few (3) inner tooth rows compared to 5 in cf. "red carp".

In all the colours of the rainbow — the *Haplochromis nyererei* complex

The *Haplochromis nyererei* complex is a rather close-knit species complex that very probably represents largely a monophyletic group, and may in a revision of the rock-dwelling cichlids of Lake Victoria be given (sub)generic status. A (sub)generic name is currently not available, because the first species of this complex was discovered and described just after Greenwood's (1980) generic revision of the Lake Victoria haplochromines. Until today *Haplochromis nyererei* Witte-Maas and Witte 1985, remained the only described species in the complex. However, meanwhile we know about 20 undescribed species, delimitation among which is not always simple (Seehausen 1996), and which I will refer to as

A female *H.* "carp" in the aquarium.

Rocky slab shore at Buyago Rocks

A male *H.* "orange carp" from Zue Island.

A male *H.* "red carp" from Buyago Rocks".

A male *H.* "red carp" from Kissenda Bay.

A male *H.* cf. "red carp" from Bwiru Island.

Nyererei species. Among the rock-dwelling Lake Victoria cichlids the complex can be characterized by the combination of the following characters (revised after Seehausen 1996): Straight to moderately incurved dorsal head profile; unequally bicuspid to unicuspid teeth in the outer tooth row (females of one species have subequally bicuspid teeth), that are in adult males coarse, with recurved crowns, and set so that the interspaces among the teeth are broader than the neck of the teeth; a rounded dental arcade; 2 to 5 rows of inner teeth; a gap between the outer and the first inner tooth row; a lower jaw length of 38-43.5 % of head length; a lower jaw length/width ratio of 1.25-1.78 (1.89 according to Witte-Maas & Witte 1985); a relatively broad head with an interorbital width of 23.6-29.1 % of head length; small deeply embedded chest scales; and a conspicuous and regular vertical bar pattern (zebra-like appearance) at least in females, with 5 to 8 bars between pectoral fin and caudal end of the dorsal fin. I think, the *H. nyererei* complex is closely related to the *Neochromis* and *Xystichromis* lineages of algae scrapers and may represent a sister taxon to them. The species complex is rather diverse in terms of feeding ecology, however, most species prey predominantly on *Aufwuchs*-associated invertebrates and/or plankton. A few species scrape predominantly algae. The most commonly used feeding techniques are picking, snapping and some scraping techniques (Seehausen et al. in press [a]). Most species exhibit pronounced sexual dimorphism in size (females being smaller) and anatomical characteristics associated with feeding.

Intragroup taxonomy among the *H. nyererei* like species and populations is complicated because the range of variation in anatomical characters in the species complex is rather narrow, and because some species do across their populations display almost the entire range of some characters. Complicating are furthermore the small geographical ranges of several species and the recurrent appearance of similar male coloration in anatomically different forms at different geographical ends

Haplochromis "zebra nyererei" lives among such shoreline boulders.

of the surveyed area. The latter observation indicates that similar male colour patterns may in cases be due to parallel evolution, rather than to shared ancestry. As a first rough approach to group species according to similarity, and independently of male coloration, I did a cluster analysis (UPGMA method) by means of which species were ordered according to similarity in morphological characters, excluding male coloration. This produced several species groups to which I will refer in the following account of the species as "morphological groups". The reader should bear in mind that these are groups, composed of species with similar shape, and that they are not necessarily particularly closely related phylogenetically, though some may well be. Thus these groups should not straight forward be understood as phylogenetic groups.

Nyererei with long heads and long jaws

The first morphological group, I call it the "Zebra nyererei group", consists of species that have a rather long head and, relative to the head length, long lower jaws. One of them, ***Haplochromis* "zebra nyererei"**, is the geographically most widely distributed species of the *H. nyererei* complex and the only one that was found throughout the surveyed area. Similar populations have occasionally been imported to Europe by aquarium fish traders from the northern lake shores. *H.* "zebra nyererei" may represent a basal member of the *H. nyererei complex*. It is the species that has the highest record of sympatric occurrences with other members of the complex, and is what I consider the matrix species of the *Nyererei* complex. It closely resembles the much better known red *H. nyererei* anatomically but has a male coloration that is strikingly different from that of *H. nyererei*: It entirely lacks any red on the body. Instead it carries its 4 to 6 vertical bars on a light grey to bright white background, creating a characteristic zebra-like appearance. The vertical bars in both sexes are usually broader and less numerous than those in *H. nyererei*. The anal fin of males is red and the caudal fin frequently features red stripes and blotches as does the dorsal fin. The teeth in the outer tooth row are in adult fishes usually unicuspid, pointed and widely spaced. The slightly longer head and lower jaw of *H.* "zebra nyererei" gives it a slightly more predatory facies than has the red *H. nyererei*. We know it from most surveyed places except the most gently sloping small boulder habitats in the Sengerema region and at Zue Island (see below). Considerable regional differences exist in coloration. For instance populations from the Mwanza Gulf and from Ukerewe do have uninterrupted vertical bars while fishes from some places in the Speke Gulf have their vertical bars rather dissolved into blotches which appear like an interrupted mid lateral and dorsal lateral stripe.

H. "zebra nyererei" is one of the most cryptically living rock cichlid species. It inhabits predominantly crevices among the rocks in shallow water (Seehausen 1996) and is only very occasionally encountered outside. In many diving hours at Makobe Island in the Speke Gulf I met it only twice: Once an adult male crossing a small stretch of sand between two heaps of rocks. The other time an adult male, standing in water of less than 1m depth, between the rocky substrate and a water hyacinth (*Eichhornia*) layer. *H.* "zebra nyererei" lives at moderately and steeply sloping shores with medium to large rock boulders but is absent from very gently sloping shores with small boulders. Its diet is dominated by benthic insect larvae, predominantly of may flies (Ephemeroptera), which it collects between the rocks. Zooplankton, small fish, and moss animals, scraped off from the rocks, are occasionally also eaten (Bouton et al. submitted).

H. "zebra nyererei" lives sympatric with most other species of the *H. nyererei* complex. There is strong evidence that all these are specifically distinct from *H.* "zebra nyererei" (but see under *H. nyererei* and *H.* "big blue"). There is little doubt also about the distinctiveness of the uniquely coloured *H.* "red head", though it is allopatric with *H.* "zebra nyererei". The situation is more complicated with a few other forms that resemble *H.* "zebra nyererei" in male coloration, and live at places at which "normal" *H.* "zebra nyererei" does not occur. Their mutually exclusive distribution with *H.* "zebra nyererei", suggests that they are representing the "zebra nyererei" lineage. However, considerable differences in morphology between these and other populations of "zebra nyererei" suggest that they could as well be derived from other species within the complex. Since, moreover, they differ also ecologically from all other populations of "zebra nyererei", I prefer not to lump them with *H.* "zebra nyererei" until more is known.

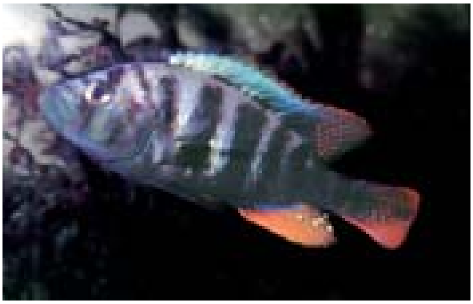
One of these populations, ***Haplochromis* "zebra Senga"**, lives at a geographically isolated rocky peninsula in the central Speke Gulf (Senga Point). It differs from other *H.* "zebra nyererei" mainly by having much shorter lower jaws, in spite of a rather long head, and bicuspid instead of unicuspid teeth in the outer tooth row. Thus it seems adapted to other feeding habits. In contrast to typical *H.* "zebra nyererei", the fishes of the Senga Point population are frequently seen moving about openly over the rocky substrate and go down to at least 5 m depth. In this respect, they resemble species like *H.* "big blue" and *H.* "red head". Morphologically they are closest to some endemics of the southern and central Speke Gulf (*H.* "blue nyererei", *H.* "red anal nyererei" and *H.* "Bwiru nyererei") and there is rather strong variation in some characters. I assume that this either is a population of *H.* "zebra nyererei" that is occupying a niche different from that of most other populations, and is therefore exposed to a quite different selection regime, or that it is a population that originated by introgression between "zebra nyererei" and one of the three above mentioned Speke Gulf endemics. All three, just like typical "zebra nyererei", are absent from Senga Point.

A second population resembling "zebra nyererei" in male coloration deviates from it in another way. ***Haplochromis* "zebra Miandere"**, living at Miandere Islands in the west of our survey area, has a much shorter head, and relative to the head length somewhat shorter lower jaws. In fact this population has one of the shortest heads found among species of the *H. nyererei* complex. Its habitat is a steeply sloping big boulder shore, and like "zebra Senga", also "zebra Miandere" is frequently seen outside of rocky crevices. Though caught in crevices as well, it is by far the most abundant haplochromine species outside of crevices, and down to at least 6 m depth, living together with *H. (Neochromis)* "blue scraper", *H.* "orange dorsal nyererei", *H.* "yellow anal nyererei" and *H.* "yellow chin pseudonigricans". It is interesting to note that all three species of the *H. nyererei complex* that live at Miandere Island, have a very short head (table 3). It may imply selective advantages of a short head in the particular environment of this island.

***Haplochromis* "red chest"** is a small form, known only from Anchor Island in the northeastern Mwanza Gulf, one of several very steeply sloping islands composed of big to huge boulders, from which typical "zebra nyererei" has not been recorded. *H.* "red chest" differs from "zebra nyererei" mainly by a shorter lower jaw and in male coloration, bearing a large orange-red area on the operculum and behind the pelvic. Moreover, its vertical bars are less dark and are on yellowish, rather than whitish flanks. The question whether "orange chest" is an aberrant population of *H.* "zebra nyererei" or a distinct species can currently not be answered. Though *H.* "red chest" seems not to coexist with the latter in sympatry, the locality of its occurrence lies within the geographical range of the latter. The population density of "red chest" at Anchor Island is low, and until today less then 10 individuals have been collected.

Morphologically close to *H.* "zebra nyererei", but a distinct species that lives sympatric with the latter at some places, is ***Haplochromis* "big blue"**. It exhibits a

Male *H*. "zebra nyererei" from Igombe Island (top) and Makobe Island (centre).



A male *H*. "zebra nyererei" from Python Is.

A female *H*. "zebra nyererei" from Python Island.

A male *H.* "zebra nyererei" from Hippo Island.

A male *H.* "zebra nyererei" from Namatembi Is.

A male *H.* "zebra Senga" from Senga Point.

A male *H.* "zebra Miandere" from Miandere Is.

particularly pronounced sexual dimorphism. Males reach a size of more than 120 mm SL and deviate from *H.* "zebra nyererei" by a steeper dorsal head profile, a shorter head, broader jaws, often bicuspid teeth in the outer tooth rows, and smaller eyes. Females do not grow bigger than 80 mm SL, have unequally bicuspid teeth in the outer rows, and more inner tooth rows than female "zebra nyererei". They retain the *H. nyererei*-like general appearance though with a steeper dorsal head profile than most other members of the complex. Full adult males, in contrast, attain a peculiar shape with indications of a nuchal bump. *H.* "big blue" is known only from the Sengerema region where it inhabits islands and some places at the mainland shore. At Chamagati Island and at the mainland shores, males are bright sky blue with 6 to 8 dark vertical bars on the flanks, and much red in the fins: anal fin, soft part of the dorsal fin and often pelvic fins. With this coloration they resemble *H. (Neochromis)* "blue scraper" and they are similarly variable in the extension of the red colour in their fins. A second, more rare male morph of *H.* "big blue" at Chamagati Island is pinkish red on the flanks between the vertical bars. Females are yellowish brown with red-brown head surface and bright yellow chin, underside, and fins. The populations from Matwinki and Juma Islands differ in morphology (bigger eyes, bigger interorbital width) but in particular in male coloration from the others. Males are not blue but pinkish red. Unlike the red morph males from Chamagati Island, the Matwinki and Juma males have their red not restricted to the flanks but it is the dorsum, dorsal fin, head surface and snout where the red is most intensive. Though the red populations have a bigger inter orbital width, and a slightly shorter head and lower jaw, and thus were in the cluster analysis of morphometric data placed closer to some other species of the *H. nyererei* complex, I consider them conspecific with the blue populations with which they share a general appearance of males that is unique in the species complex, as well as the small yellow females.

Most habitats of both, the blue and the red form of "big blue", consist of very gently sloping shores with small rock boulders and rubble substrate. *H.* "big blue" is found from very shallow water down to at least 4 m depth. The very big fully adult males are restricted to the deeper parts of the species´ depth range and can easily be taken for a separate species, particularly since females are rarely caught together with them at depths below 1.5 m. Females and smaller males live predominantly in the shallow water. We caught females almost exclusively at less than 1.5 m depth. Males of 10 cm SL become already territorial in the shallows. Both sexes feed here predominantly on epilithic *Aufwuchs*, and the most frequently used feeding techniques are pullscraping and picking (Seehausen unpubl. data). The algae scraping habit of *H.* "big blue" is unique among the known *H. nyererei* complex species. Like many algae scrapers of other species complexes, it inhabits with high population densities the shallow waters, and is among the numerically dominant species at several places, following in abundance after *H. (Xystichromis)* "copper black" and *H. (Neochromis)* "black nigricans". Most other *H. nyererei complex* species live either in deeper waters or in crevices between the rocks. At Juma Island most of the shore consists of bigger, steeper sloping boulders. However, "big blue" does occur there at the most gentle places down to at least 4.5 m depth. Its population density is there much lower than at the very gently sloping small boulder islands.

H. "big blue" coexists with four other *H. nyererei complex* species: *H.* "all black nyererei", *H.* "pink anal", *H.* "zebra nyererei" and *H. nyererei* (with the latter two only at Juma Island). Some variation between its populations exists. So do the fishes from the mainland have more an insectivorous dentition than the fishes from Chamagati Island. At several rocky mainland shores of the Sengerema region, between Kujunju Point and the Mwanza Gulf entrance, we found populations that are intermediate between *H.* "big blue" and *H.* "zebra nyererei" in coloration and anatomy (abbreviated cf. Zny-Bbl in the distribution map). Some of these populations are either very variable or represent an admixture of two species: *H.* "big blue" and *H.* "zebra nyererei", converging towards an intermediate phenotype, or actually hybridizing. These observations may suggest that *H.* "big blue" is closely related to *H.* "zebra nyererei", despite different feeding ecology and trophic morphology. Along the Sengerema mainland shore, typical "big blue" are found at very gently sloping small boulder shores, while the variable populations that are intermediate between "big blue" and "zebra nyererei", live at shores that have bigger boulders and slope slightly steeper. Typical "zebra nyererei" inhabit steeper sloping rock shores with boulders large enough to create a rich interstitial of crevices. More ecological work on these populations will be needed to clarify these interesting patterns but it seems that the two forms, in one way or the other, replace each other ecologically. It is particularly interesting that at Juma Island, "zebra nyererei" and the red form of "big blue" live in sympatry, and that no intermediate forms are found at this island.

If "big blue" is considered the representative of the "zebra nyererei"-lineage at gently sloping shores, than it is furthermore important to note that it lives sympatrically with a second species that is similar to *H.* "zebra nyererei", though grouped in a separate morphological group: ***Haplochromis* "all black nyererei"**. This is a rare species, of which we caught 12 individuals at Chamagati Island and at Kajunju Point (Sengerema mainland). Males are entirely black with a reddish anal fin and often rather dull orange coloured egg dummies. Females are blackish brown. It lives at depths between less than a metre and at least 4 m, and has been caught only at very gently sloping shores. Nothing more is known yet about its ecology. *H.* "all black nyererei" shares with *H.* "zebra nyererei" a long head.

In fact this species has the longest head found among *H. nyererei complex* fishes but it has at the same time one of the shortest lower jaws found among them, and so *H.* "all black nyererei" differs in this respect considerably from "zebra nyererei". Morphologically "all black nyererei" is similar to *H.* "zebra Senga". It lives sympatrically with at least two other *Nyererei* complex species, *H.* "big blue" and *H.* "pink anal".

Morphologically and ecologically most similar to *H.* "big blue" is ***Haplochromis* "red head nyererei"** that is entirely different in male coloration. It is another non-cryptically living shallow water dweller. Known only from two islands in the central-northern Speke Gulf, it is very abundant at Zue Island, much less so at Mabibi Islands. Zue Island has a very gently sloping shore with small rocks and stones, while Mabibi Islands have medium steep slopes and very different rock substrate (see the chapter about habitats). The two populations differ anatomically, those of Mabibi Islands being more elongated and having a shorter head than those from Zue Island, but they are almost identical in their brilliant male coloration. Snout, cheek, branchyostegal membrane, gill cover, chest and anterior parts of flanks and belly are deep blood red, the posterior parts of the flanks and the caudal peduncle are greenish, the dorsum yellowish. The dorsal fin is metallic blue with red dots and streaks to entirely red. The caudal fin is reddish, the anal fin blue around the egg dummies, and reddish on the spinous part. Females are yellowish, though not as yellow as those of *H.* "big blue". Both sexes have 6 to 7 (rarely 8) vertical bars on the flanks. Males differ from those of *H.* "all red nyererei" and *H.* "red flank nyererei" by the different topographical arrangement of colours on head and body, and by the blue and red instead of orange coloured anal fin. Moreover, the other two do not belong to the group of species with a long head and long lower jaws. The body shape of *H.* "red head" is similar to that of *H.* "big blue" but is usually less deep, and with a less steep dorsal head profile. *H.* "red head" seems to remain considerably smaller.

H. "red head" lives at Zue Island between the surf line and 5 m water depth, openly on the rock substrate, moving sometimes in mixed shoals with algae scrapers of the *Neochromis* lineage. At Mabibi Islands we observed it between 1 and 4 m water depth among boulders as well as moving freely across the rock bottom. Within the available range of microhabitats at Mabibi, it seems to prefer the less steeply sloping areas. *H.* "red head nyererei" is the only *H. nyererei complex* species at Zue Island but coexists with *H.* "blue nyererei" at Mabibi Islands.

Plankton eating *Nyererei* with a broad head

In a second morphological group, let it be called the "red nyererei group", species are joined that share a rather broad head (big interorbital width) and a medium long lower jaw. Many of them are shoaling inhabitants of either the water column above the rocky substrate, or of wide and deep gaps among big rock boulders. However, also the red form of *H.* "big blue" fell in the morphological analysis into this group, as did *H.* "Miandere zebra", which I regard as close to *H.* "zebra nyererei". With the exception of these, all species in this group share a dark body coloration, and bright yellow, orange or red fins. In the case of *H. nyererei*, the bright red includes the dorsal aspects of the body. I propose the following hypothesis concerning the ecological significance of this coloration pattern. All species with this type of coloration about which information from Scuba observations is available (*H. nyererei*, *H.* "black and orange nyererei", *H.* "lemon fin nyererei", *H.* "orange dorsal nyererei"), have ecological and behavioural traits in common: all are predominantly plankton feeders, the females of which forage in shoals in the water column above the rocks. Males have their spawning territories on the rocky substrate, and have to approach and court their females from beneath. Females see territorial males mostly from above. Conspicuously coloured body outlines, in particular dorsal and caudal

Chamagati Island, habitat of *Haplochromis* "big blue".

A territorial male *H.* "big blue" from Chamagati Island.

A female *H.* "big blue" from Chamagati Is.

A red male *H*. "big blue" from Matwinki Island.

A territorial male *Haplochromis* "red head nyererei" in the aquarium.

A male *H*. "all black nyererei" from Chamagati.

A female *H*. "red head nyererei"

A male *H*. "red head nyererei" from Mabibi Is.

A male *H*. "red head nyererei" from Zue Island.

fins, but also the anal fin that is held somewhat aside of the longitudinal axis of the body during quiver display and lead swimming, may in such situations be more "eye-catching" to the female than, for instance, flank coloration. I propose the term "body outline coloration" in contrast to "body centre coloration". The latter occurs in many species of the "zebra nyererei" and the "blue nyererei groups" and a good example is *H.* "red head nyererei".

Haplochromis nyererei Witte-Maas & Witte 1985 is the only described species in the *H. nyererei* complex, and at the same time one of the most conspicuous of all Lake Victoria cichlids. It has a somewhat disjunct geographical distribution, living in the Mwanza Gulf, at a few places along the southern Speke Gulf shore, and at two offshore islands in the Speke Gulf (Makobe and Ruti Islands). It is absent from other places at the southern shores of the Speke Gulf, as well as from the more eastern and northern Speke Gulf islands, the northern Speke Gulf shore, and from the region west of Juma Island. However, at Gana Island northwest of Ukerewe we collected fishes that resemble it, and may well be *H. nyererei*. Furthermore, it has been reported even from the Kenyan lake shore (Kaufman & Ochumba 1993) and a photograph of that population has recently been published (DeMason 1996a). Judging from this photo, the Kenyan fishes differ from those from the southern lake shores, but may indeed belong to the same species. In the Mwanza Gulf south of Python Islands, populations are found that are intermediate between *H. nyererei* and *H.* "zebra nyererei" (see below).

H. nyererei is morphologically similar to *H.* "zebra nyererei", the most conspicuous difference being male coloration. Males exhibit a bright orange-red to crimson-red head, dorsal fin and dorsum, the red colour extending downwards on the flanks to below the lateral line, a lemon yellow anterior flank region and black or blue (depending on the population) lower jaw, cheeks, gill cover, and lower side. Females are light brownish. Both sexes have 6 (rarely 5) to 8 vertical bars on the flanks. The description of *H. nyererei* (Witte-Maas and Witte 1985) was based on fishes from two geographically nearby and morphologically similar populations, Mushroom and Kilimo Islands in the northeastern Mwanza Gulf. Now, that *H. nyererei* has been collected from many other places, we know that morphological variation between populations is considerable in both sexes, particularly regarding body depth, lower jaw length and width, as well as details of male coloration. Fishes from Ngoma Point, Python, Nyamatala and Kissenda islands in the Mwanza Gulf are deeper bodied than those from Nyegezi rocks (Mushroom Island is part of the Nyegezi rock peninsula), Anchor Island, Ascari Island, Capri Point, Igombe, Makobe and Ruti Islands. Males of the deep bodied form have sky blue underparts, those of the other one have black underparts. Females of the first are lighter yellowish brown than those of the second. Similar to the deep bodied populations from some places in the Mwanza Gulf is the population from Senga Point in the central Speke Gulf. It is separated from that of Kissenda Island by more than 40 km shoreline which at several places is inhabited by populations of the shallow bodied, more elongated type. We do not yet know whether such similarities and differences among *H. nyererei* populations reflect population phylogenetic patterns or repeatedly evolved adaptations to local environmental situations.

H. nyererei lives in sympatry with *H.* "zebra nyererei" throughout its geographical range, with *H.* "black and orange nyererei", *H.* "Bwiru nyererei", *H.* "red rim anal", and *H.* "pink anal" at Igombe Island, with *H.* "pink anal" also at Makobe Island, with *H.* "blue nyererei" at Ruti Island, and with the red form of *H.* "big blue" at Juma Island. *H. cf. nyererei* of Gana Island coexists with *H.* "lemon fin nyererei" and *H.* "all red nyererei". *H. nyererei* and *H.* "zebra nyererei" occupy different microhabitats, though at some places with considerable overlap. It has been shown that they mate assortatively (females of the red form mate with red males, those of the "zebra" form with "zebra" males) and behave as two biological species over much of their common geographical range. However, in the southern Mwanza Gulf, south of Python Islands, they seem to behave as two interbreeding colour morphs of a single species and individuals of all intermediate colour types exist (Seehausen 1996, abbreviated cf. Zny x Nye in the distribution map). At Makobe Island entirely black males are frequently found among the normal red ones (see photo). Because intermediate phenotypes also occur which are black with some red on the dorsal head surface, dorsum, or dorsal fin, and because no ecological differences between the morphs have been observed yet, I consider the black and the red males as colour morphs of one species. However, behavioural experiments, like those done with *H. nyererei* and *H.* "zebra nyererei", are desirable to confirm this.

H. nyererei populations vary also ecologically. At most places *H. nyererei* is predominantly zooplanktivore, however, at Ruti Island it is predominantly phytoplanktivore and at Anchor Island benthivore, eating mostly insect larvae and prawns (Bouton et al. submitted). It inhabits predominantly slightly deeper waters below 2m depth and has been observed down to 14 m depth at Ruti Island in the Speke Gulf. At steeply sloping shores it occurs also in water shallower than 2 m immediately inshore, and even in crevices among the rocks at the surf line. At moderately steep shores it can be confined entirely to the deeper parts of the rocky habitat, and at very gently sloping shores it is absent, possibly because at such places rock substrate makes way for sand before a suitable depth is reached. At most localities, *H. nyererei* is among the numerically dominant haplochromines in its major habitat and seems to dominate other planktivorous species where they coexist. Females, subadults, and nonbreeding males of open water dwelling (plankton eating) populations forage in shoals, sometimes directly above the rocks, sometimes several metres higher in the water column, probably following the highest plankton densities. At Makobe Island I had the opportunity to observe such foraging shoals in some detail at 4 to 6 m depth. They consisted of ten to over a hundred individuals that varied relatively little in size. I saw shoals containing only fishes of 3 to 5 cm SL and others with only larger individuals. When grazing plankton, the shoals were stationary and moved often no more than a few metres in an hour. The plankton (copepod) density was so high that a fish would almost permanently, and with hardly any locomotion, perform the cyclus of sucking-in, processing, and swallowing. During plankton grazing, individuals kept some distance to each other but closed up, as soon as the shoal was disturbed and moved on. Adult reproductively active males become territorial, and at Makobe Island defend areas of about 1.5 m diameter. These territories are frequently centred around rocks that are slightly larger than the average, and that are surrounded by also slightly deeper crevices. Brooding females do not stay inshore in shallow waters like the brooding females of many *Neochromis* and *Xystichromis* do, but keep to deeper parts of the rocky shores below 4 m depth where they defend small territories. These consist usually just of a crevice between some rocks. Such territorial females are very dark brown. In spite of their small size (often no more than 5 cm SL) they are very aggressive and successful defenders of their offspring.

Anatomically very similar to the elongated form of *H. nyererei* is ***Haplochromis* "black and orange nyererei"**, which is very different in coloration. Males are deep black or brown-black, with anal, caudal, and often pelvic fins bright orange, and the dorsal fin black with orange lappets. They can show a trace of orange on the neck. Females are dark and more grey-brown than *H. nyererei* females. This species may grow a little bigger than the elongated form of *H. nyererei*. Many males have filament-like extended pelvic fin rays. The lower jaw width is very variable within populations. We know *H.* "black and orange nyererei" from three places at the southern mainland shore of the Speke Gulf. It resembles *H. nyererei* in its ecology. We found it at moderately steep and steep shores with medium sized to very big rock boulders. At steep shores it inhabits already immediately inshore waters where it lives in deep and wide gaps between big boulders, while at the moderately steep shore of Igombe

A territorial male *Haplochromis nyererei* from Igombe Island.

A male *H. nyererei* from Python Island.

A female *H. nyererei* from Ruti Island.

A male *H. nyererei* from Makobe Island

An orange male *H. nyererei* from Igombe Is.

A male *H. nyererei* from Senga Point.

A male *H. nyererei* from Nyegezi Rocks.

A black male *H. nyererei* from Makobe Island.

A male *H. nyererei* from Anchor Island.

A male *H.* "black & orange nyererei" from Ndurwa Point.

Island it is confined to slightly offshore areas of beyond 2 m depth. Males occupy territories at 3-4 m water depth and deeper, among big boulders, from where they court bypassing or foraging shoals of females. The stomachs of four males (two of the orange fin morph, two of a red fin morph) from Igombe Island that we examined, contained unexpected items. Two individuals (one of each morph, see below) had fed almost exclusively on filamentous green algae and some blue-green algae. The other two had small amounts of algae as well, but predominantly detritus consisting of macerated macrophyte tissue. No traces of zooplankton were found. From Scuba work I know that the plant material is of rotting water hyacinths (*Eichhornia crassipes)* that form many centimetre thick layers at the southern Speke Gulf rocky mainland shores since about one to two years ago. Before 1995 the rocks at these shores were rather free of detritus.

The very close anatomical and ecological resemblance between *H.* "black and orange nyererei" and *H. nyererei* suggests that the two are closely related. They may have evolved as geographical vicariants. However, their current distribution is not entirely exclusive. At Igombe Island, both species live in sympatry. The red *H. nyererei* is there much less abundant than "black and orange" but its abundance seems to either have increased very recently, or to undergo considerable fluctuations over several years. Some of the red *H. nyererei* males that we found there seem to bear some characteristics typical for *H.* "black and orange nyererei" (more orange than red colour, filamentously extended pelvic fins). Thus, occasional hybridization between the two forms cannot be excluded. However, since both forms clearly maintain their phenotype in sympatry, I consider them as two species. *H.* "black and orange nyererei" furthermore lives sympatrically with *H.* "zebra nyererei", *H.* "Bwiru nyererei", *H.* "pink anal" and *H.* "red rim anal". At Igombe Island and Ndurwa Point we caught four males of a colour morph with wine red instead of orange fins that otherwise resemble the orange fin males in morphology but are similar in coloration to *H.* "red anal nyererei" of the Vesi archipelago in the central Speke Gulf.

Populations that differ considerably in general appearance and morphology from *H.* "black and orange nyererei", but whose male coloration is similar to that of the latter, occur far away from the range of *H.* "black and orange nyererei" at steeply sloping big boulder shores in the Sengerema region (Bihiru and Miandere Islands: *H.* "orange anal nyererei", *H.* "small mouth nyererei") and at Gana Island north of Ukerewe (*H.* "lemon fin nyererei"). These similarities may well be due to parallel evolution of male nuptial coloration under similar environmental light conditions. This in particular since a very similar colour pattern also occurs in species of the *Haplochromis* "pseudonigricans" complex (see below). Future research must show whether this hypothesis holds true.

The two populations of black and orange coloured fishes from the Sengerema islands Bihiru and Miandere fell into one morphological group with *H. nyererei* and *H.* "black and orange nyererei". Nevertheless, they are in general appearance and lower jaw length/width ratio not only that much different from each other, that I consider them two different species, but ***Haplochromis* "small mouth nyererei"** of Miandere Islands differs from all other *H. nyererei* complex species in general appearance. It is very deep bodied and does with its small snout resemble species of the *H.* "pseudonigricans" complex. Another peculiarity of this species is the large number of egg dummies that occupy much space on the anal fin of the male. Males are black with a bright yellow anal fin, yellow dorsal fin lappets, and a caudal fin that is orange coloured in its distal most third. Females are brown with about seven narrow vertical bars on the flanks. At Miandere Islands *H.* "small mouth nyererei" lives at water depths ranging from 3 to at least 6 m. It lives in sympatry with *H.* "Miandere zebra" and *H.*

"orange dorsal nyererei" as well as with a population of *H.* "yellow chin pseudonigricans" that has a male coloration similar to that of *H.* "small mouth nyererei".

At Bihiru Island, separated from the Miandere Islands by about 10 km of maximum 40 m deep water, lives ***Haplochromis* "orange anal nyererei"**. In coloration it hardly differs from "small mouth nyererei". Males are a bit more blueish, the fin colour is more orange than yellow and the egg dummies are fewer on the anal fin. The vertical bars on the flanks, particularly of females, are broader than those of "small mouth nyererei". Occasionally males are encountered with an anal fin that is black and has only a narrow orange coloured rim. The species is with up to 125 mm SL one of the largest members of the complex. It lives in crevices among big rock boulders at only one metre depth, as well as at the steep slope outside of crevices down to at least 9 m depth. It is the second most abundant haplochromine species at the steep shores of Bihiru Island (after *H. (Neochromis)* "Bihiru scraper"). *H.* "orange anal nyererei" lives sympatrically with *H.* "zebra nyererei" that, however, is restricted to crevices in shallow water, and with *H. cf.* "orange dorsal nyererei" that is very rare at Bihiru and was collected only once in water of about 7 to 9 m depth.

The last species in this morphological group is ***Haplochromis* "Ukerewe nyererei"**. This is a species of the southern Ukerewe area, known from Ukerewe Island itself (Nansio) as well as from Bwiru Island, that in ecology (i.e. microhabitat distribution) and morphology closely resembles *H. nyererei*. In male nuptial coloration it is quite different from the latter and more similar to *H.* "zebra nyererei" (with which it lives in sympatry) and *H.* "black and orange nyererei". Males are dark metallic blue with black vertical bars on the flanks. The anal fin, outer third of the caudal fin and dorsal fin lappets are either crimson or orange coloured. Females are grey-brown with metallic silvery iridescent spots on the flank scales. Both sexes bear, like in *H. nyererei,* 6 to 7 narrow vertical bars on the flanks. At Nansio Island, a rocky hill, separated from the main Ukerewe Island by water of just about 20 m width, this species lives between 3 and at least 5 m depth over medium sized and big boulders, while rocky crevices in shallow water are inhabited by *H.* "zebra nyererei". At Bwiru Island *H.* "Ukerewe nyererei" lives at depths between less than 1 and at least 7 m. Its population density is particularly high at about 4 m depth, in a partly surf exposed area. It is frequently encountered also in rocky crevices, together with *H.* "zebra nyererei". The latter species is at Bwiru Island much more rare than at Nansio.

Plankton eating *Nyererei* with a short and broad head

A third morphological group, "lemon fin group", consists of only two species, *H.* "lemon fin nyererei" and *H.* "orange dorsal nyererei", that have a very short and very broad head (large interorbital width) in common. Judging from male coloration ("body outline coloration") they are very close to the group with *H. nyererei* and *H.* "black and orange nyererei". However, since they are also ecologically similar to these species, living in very similar microhabitats, the resemblance in male coloration may as well be due to parallel evolution. ***Haplochromis* "lemon fin nyererei"** lives at the island archipelago northwest of Ukerewe, where we found it at Gana Island. Possibly it is more widely distributed along the western shores of Ukerewe and/or further north. Reaching more than 130 mm SL in the male sex, it is the largest species known in the *H. nyererei* complex. Adult males are of a very distinct appearance. They are deep bodied and have a relatively steep dorsal head profile, comparable to that of big *H.* "big blue" males. With this, and with a relatively broad lower jaw, they are morphologically very different from *H.* "black and orange nyererei", a species to which "lemon fin" is close in coloration. Males are grey with six dark vertical bars to entirely black. The anal fin, almost the entire caudal fin, and the lappets of the dorsal fin are lemon yellow. Females are grey-brown with six to seven vertical bars on the flanks and have lemon yellow dorsal fin lappets as well.

"Lemon fin" inhabits in rather high abundance the fantastic rock gardens of Gana Island. There it lives in large shoals of females and subadult males in deep canyons, steep "wells" and several metre deep and wide caves among big to huge rock boulders. As a diver, one usually sees these shoals foraging on plankton, for

A male *H.* "small mouth nyererei" (Miandre).

A female *H.* "small mouth nyererei" (Miandre).

A male *H.* "orange anal nyererei" (Bh).

A female *H.* "orange anal nyererei" (Bh).

A male *H.* " Ukerewe nyererei" (Bwiru Is.).

A female *H.* "Ukerewe nyererei" (Bwiru Is.).

A male *H.* "orange dorsal nyererei" from Miandere Islands.

A male *H.* "lemon fin nyererei" from Gana Island.

which they disperse over several metres depth in the water column of "wells" and canyons, sometimes occupying a whole "well". While plankton grazing, the individuals in these shoals keep several centimetres distance from each other, and remind the observer of the plankton grazing shoals of *Neolamprologus brichardi* in Lake Tanganyika. When disturbed by a diver the shoals withdraw into the large caves that are characteristic for their habitat. Adult and reproductively active males live differently: they defend territories around rock holes, in front of which they display upwards into the water column to the shoals of females that forage above them. Thus their behaviour is very similar to that described above for *H. nyererei*. Like the males of the latter, do also "lemon fin" males "jump" up into the lower parts of female shoals, to perform a lateral display and a quiver, and return to their cave in lead swimming position. When observing this courtship dance from above, a diver sees not more than yellow flashes, flickering around the female shoals. *H.* "lemon fin nyererei" lives at water depths from 2 to at least 5 m. The territories of the males are at depths of 4 m and beyond. The species lives sympatrically with three other species of the *H. nyererei* complex: *H. cf. nyererei*, *H.* cf. "zebra nyererei" and *H.* "all red nyererei".

***Haplochromis* "orange dorsal nyererei"** lives at the Sengerema islands Miandere and possibly Bihiru (identification of the fishes from Bihiru has still to be confirmed). It may be more widely distributed west of the surveyed area. Similar to *H.* "small mouth nyererei", which lives together with it at Miandere, this species has a short, and yet narrow lower jaw, and thus a small mouth. The "body outline coloration" of this species is reduced to a broad orange band in the dorsal fin, orange caudal fin corners and a pale yellowish white anal fin edge. The orange dorsal band is so vividly coloured that it appears almost fluorescent. The body is not entirely black as in *H.* "black and orange nyererei" and similar species, but more grey-brown, with usually five broad black vertical bands on the flanks. At Bihiru and Miandere Islands "orange dorsal nyererei" lives at open steep slopes with big and huge rock boulders. At Bihiru it was collected only once at about 9 m depth. At Miandere we collected adult males in nets at depths of circa 4 to 6 m, and observed subadults and females in mixed shoals together with *H.* "yellow chin pseudonigricans" which have a very similar coloration. When these shoals are seen from above by a diver, it is often only the orange dorsal bands that are visible like fluorescent light against the very dark coloured rocks. *H.* "orange dorsal nyererei" lives sympatrically with *H.* "Miandere zebra" and *H.* "small snout nyererei".

***Nyererei* with narrow heads and short jaws**

The last morphological group within the *H. nyererei* complex, let it be called the "blue nyererei group", consists of species that share short lower jaws and a rather narrow head (small interorbital width). Most seem to be substrate oriented feeders. Judging from general appearance and male coloration this group again can be split into two. One has reddish males, the other one blueish to blackish males. Endemic to islands in the central Speke Gulf is ***Haplochromis* "blue nyererei"**. Males from Vesi and Mabibi Islands are dark metallic blue with a bright metallic blue dorsal fin, and a proximally blueish, but distally often pale reddish caudal fin. The anal fin is proximally black, followed by a pale silvery iridescent zone and is distally faint red. The egg dummies are few and pale yellow. The anal fin coloration helps to distinguish "blue nyererei" from the sympatrically and partly syntopically living, rather dull coloured Vesi Islands population of *H.* "zebra nyererei". The latter has a red anal with often many orange coloured egg dummies. Furthermore, its flanks are more brownish rather than blue. Females of *H.* "blue nyererei" are light brown with iridescent blue spots on the flank scales and have a greyish-yellow anal fin. They are more elongated than the females of *H.* "zebra nyererei" and have a characteristic head shape. Their snout appears (compared to that of other *Nyererei*) too short for the slenderness of body and head, and gives the impression that the fish has got a "blow on its nose". Females usually bear five, males six rather broad vertical bars on the flanks. Males from Ruti Island are generally darker blue-black coloured but otherwise like those from the other islands. The population from Sozihe Island differs from the others mainly in male coloration. These fishes are rather dull dark grey to black, the lips often being the only blue part of the body. The red colour of the anal fin is frequently more intensive. Some big males from Sozihe Island have a "zebra nyererei"-like general appearance. Typical *H.* "zebra nyererei" have not been found at Sozihe Island, and I cannot exclude the possibility that they form here an introgressive population with *H.* "blue nyererei" (compare with the situation at Senga Point, page 103). Although one of the smallest species in the *H. nyererei* complex, males of "blue nyererei" have in the outer tooth row rather stout, widely spaced unicuspid teeth which are often recurved. Small males and females sometimes have some weakly bicuspid teeth.

Little is known about the ecology of *H.* "blue nyererei". It lives at moderately steep to steeply sloping large boulder shores, where it inhabits crevices between the rocks in shallow water, as well as the open slope down to greater depths. Its microhabitat distribution differs among islands, and circumstantial evidence suggests that these differences in microhabitat distribution are caused by some sort of interference with other members of the *H. nyererei* complex. At Sozihe Island *H.* "blue nyererei" is abundant in all microhabitats, in rock holes and on the slope from shallow water to at least 5 m depth. It is the only species of the *H. nyererei* complex at Sozihe. At Mabibi Islands females and subadult males are among the most abundant fishes in the shallow littoral of 1 to 2 m depth over slabs and among boulders, but reach down to at least 12 m depth. Adult males live between 2 and at least 12 m depth and are there by far the most abundant cichlids. The only other species of the complex at Mabibi islands is *H.* "red head nyererei", which is quite rare and numerically dominated by *H.* "blue nyererei". In the Vesi archipelago, "blue nyererei" is the numerically dominant haplochromine at many small, steeply sloping islets. It lives there in the crevices among big boulders, and at the slope of these boulders, between 1 and at least 6 m depth. In contrast, it is rare at the moderately steep slopes of the main island. At the steep islets it coexists with *H.* "zebra nyererei" but this one is restricted to crevices, and is even there outnumbered by "blue nyererei". In contrast, the moderately steep slope of the main island is densely populated by *H.* "red anal nyererei". At Ruti Island *H.* "blue nyererei" is restricted to depths beyond 8 m. The crevices in shallow water at Ruti are populated by *H.* "zebra nyererei", and the open slope by *H. nyererei* that occurs in great abundance from the shallows to about 12 m depth. *H. nyererei* and *H*. "blue nyererei" seem to have similar microhabitat demands for the establishment of territories. Both species settle at Ruti Island in great density on the only slightly sloping rock rubble ground that exists at the foot of the steep cliff, from about 10 m depth downwards. However, territories of *H. nyererei* are also found at lesser depths among the boulders and this species numerically dominates on the rubble shelf down to 11 m depths, while below that the ratio turns in favour of *H.* "blue nyererei". Territorial males of the latter occur down to at least 14 m depth. Territorial density at Ruti Island is very high and territories are relatively small, those of *H. nyererei* seem to be larger than those of *H.* "blue nyererei". At Mabibi Island territorial *H.* "blue nyererei" males are observed already in 6.5 m depth. Their territorial density is little compared to that at Ruti Island and their territories are either not bordering each other or are larger than at Ruti Island, all indications of lower competitive pressure. These observations indicate that the restriction of *H.* "blue nyererei" to very deep waters at Ruti Island may be explained by its competitive inferiority to *H. nyererei*. Competitive interference with other species may also explain the absence of "blue nyererei" from mainland shores of the Speke Gulf. We once caught one male at Igombe Island that resembled the Ruti Island population, implying that the species occasionally reaches mainland rock shores but does not establish populations there.

Territorial males of *H.* "blue nyererei" at Ruti Island court females in much the same manner as described above for *H. nyererei*. Females of both species live in mixed shoals. While plankton grazing, these shoals stay usually about 2 to 3 m above the substrate and are courted by males of both species. At 10 m depth the metallic blue dorsal fin of *H.* "blue nyererei" appears black as does the body of the fish, but the pale anal fin and caudal rim appear light whitish and are well visible.

In the Speke Gulf west of Ruti Island and in the Sengerema region *H.* "blue nyererei" is replaced by a similar species, ***Haplochromis* "pink anal"**. Though it differs just slightly from "blue nyererei" in the morphometric measurements that I took, large males of this species are not readily recognized as members of the *Nyererei* complex. This is probably due to the steep dorsal head profile and the small eyes. Due to the combination of morphological analysis, analysis of distribution patterns and behavioural observations by Scuba, it became apparent that "pink anal" is a member of the *Nyererei* complex and probably closely related to "blue nyererei". The recent discovery of the much smaller females confirmed this classification.

Young males can be blueish but full adults are deep black and have a very characteristic anal fin coloration that is unique among the known *Mbipi* species, but similar to that of "blue nyererei". The anal fin is bright pink between the hard spines. Behind the spinous part of the fin the pink gradually fades away making place for white with a faint pink flush. The small yellowish egg dummies are situated along the interface between the white distal part of the fin and the dark grey fin basis. The caudal fin is blackish with a pink margin of irregular width, the black dorsal fin has pink lappets.

H. "pink anal" inhabits mostly gently sloping shores with medium sized to small rock boulders. At islands and in mainland habitats in the Sengerema region we caught most of our "pink anals" in shallow water of less than 2.5 m depth, at Igombe Island and nearby mainland in the Speke Gulf at depths between 2.5 and 6 m. At Makobe Island, where we could study the species in some more detail, it is also found in low densities in shallow water but it becomes suddenly abundant at depths beyond 4 m. Scuba observations revealed that "pink anal" lives at Makobe Island a life very similar to that of "blue nyererei" at Ruti Island, about 10 km further east. Syntopically with *H. nyererei*, males defend spawning territories on the weakly sloping rock bottom. While *H. nyererei* numerically dominates down to 5.5 m depth, the ratio changes in favour of *H.* "pink anal" beyond 5.5 m. In the relatively dark spawning habitat of "pink anal", the pale pinkish-white anal fin is well visible, just like the pale fin of "blue nyererei" at Ruti Island described above.

I observed females and subadult males of "pink anal" foraging on plankton in shoals, mixed with *H. nyererei*, several metres above the bottom. Of seven males that we checked, four had eaten almost exclusively zooplankton (copepods), one exclusively may fly (Ephemeroptera) larvae, one almost exclusively filamentous green algae (*Cladophora*) and the last one detritus, may fly and chironomid larvae. Only the last two had sand grains in their stomach, reflecting their benthic feeding. Thus the food demands of "pink anal" seem to be quite similar to those of *H. nyererei* and competition between the two species appears possible.

Superficially "pink anal" can easily be

A male *H.* "blue nyererei" from the Vesi Islands.

A female *H.* "blue nyererei" (Vesi Islands).

A male *H.* " blue nyererei" from Mabibi Is.

A mixed school of *H. nyererei* and *H.* "blue nyererei" at a depth of 14 metres at Ruti Island.

confused with *H. (Xystichromis)* "copper black", with whom it lives sympatrically throughout its known geographical range. However, it differs from the latter in coloration and dentition. The superficial resemblance with "copper black" is also the reason for the late discovery of ***Haplochromis* "red rim anal"**, a form that is anatomically much more similar to "pink anal" and "blue nyererei", and inhabits the rocky mainland shores of the southern Speke Gulf. It is the largest of the three species and the one that gets the deepest body and steepest dorsal head profile. Large males are deep grey to blue-black with about seven black vertical bars on the flanks. All fins are black, the dorsal has red lappets and the caudal a narrow red edge that is more regular than in the other two species. Most distinct is the anal fin that is grey to black with a very sharply demarcated deep red rim along its distal mar-


The southern islet at Mabibi Islands, the habitat of *H.* "blue nyererei" and *H.* "red head nyererei".


A male *H.* "pink anal" from Makobe Island.


A male *H.* "pink anal" in the aqaurium.

gin. With this coloration the anal fin can almost certainly not function as the "light spot" in deep waters, that the pale silvery metallic or whitish anal fins of the two similar species are. Indeed does "red rim anal" live in quite different habitats. It is found at gently to steeply sloping places with small to big boulders and lives at water depths between 2 and 6 m. At Ndurwa Point we found a particularly high population density of this species at about 3-4 m depth among large rock boulders, were it co-dominates the haplochromine community, alongside with *H. (X.)* "copper black" and *H.* "black and orange nyererei". Scuba observations in that habitat did not reveal evidence for shoaling behaviour as displayed by "blue nyererei" and "pink anal".

H. "red rim anal" and the sympatric *H. (X.)* "copper black" can be told apart by male coloration (*H.* "copper black" males have the largest part of the anal fin red) as well as by morphology (the lower jaw is broader in the latter, the teeth subequally rather than weakly bicuspid and unicuspid, and the inner rows are more; see table 3).

It seems likely that the three species *H.* "blue nyererei", *H.* "pink anal" and *H.* "red rim anal" are derived from one common ancestor, although between the first and the third one the assumed close relationship becomes evident just when the second one is considered as an, in some characters, intermediate form. The major argument for considering the three, largely allopatric forms specifically distinct, is that the variation among them in morphology and coloration is geographically discontinuous. The forms of Vesi, Mabibi and Ruti islands are as unambiguously assignable to "blue nyererei" as are those of Makobe Island and the Sengerema region to "pink anal" and those of the southern Speke Gulf mainland shores to "red rim anal". The forms are not connected by a cline along a geographical gradient, neither do they represent phenotypes along an ecological gradient. There is no consistent correlation between habitat characteristics and phenotype expression. Nevertheless, it is possible that adaptation to different ecological situations has played a role in the evolution of the sibling trio and that the ecological impact has partly been masked by subsequent expansion of geographical and ecological ranges. Though the three forms rarely occur sympatrically, all three have been recorded from Igombe Island.

Morphologically very close to *H.* "blue nyererei" is also ***Haplochromis* "red anal nyererei"**. It is known only from the main island and some islets in the Vesi archipelago where it lives sympatrically with *H.* "blue nyererei" but inhabits a different microhabitat (see above). It has, like the latter, a rather elongated body shape but adult males are black with an entirely bright red anal fin, a red caudal fin rim and red dorsal fin lappets. Distribution and brightness of the red colour is reminiscent of the "body outline coloration" in species of other morphological groups, however, it is unlikely that in deeper water the relatively dark red has a similar effect. Males in nonbreeding dress have about six vertical bars on the flanks. Though males are quite common, females have not yet been found. *H.* "red anal nyererei" inhabits predominantly moderately steep slopes with medium sized rock boulders, and depths between 3 and 5 m. It is completely absent from some steeply sloping large boulder islets. A morph with red fins that is similar to *H.* "red anal nyererei" in coloration, frequently occurs among *H.* "black and orange nyererei" at Igombe Island and Ndurwa Point. It agrees in morphometrics with "black and orange" and not with "red anal", and may either represent a morph of *H.* "black and orange nyererei" or populations of *H.* "red anal nyererei" that, living under the same conditions, have converged to the morphotype of "black and orange".

The fifth species in this group is ***Haplochromis* "Bwiru nyererei"**. With its elongated body and short head it deviates from the typical *H. nyererei* shape. The head shape of adult males tends to resemble that of some algae scrapers with a slightly incurved dorsal head profile. Males are rather dull blue-grey, with variable amounts of faint red in anal and caudal fins. Females are more conspicuously coloured, being yellowish brown to brassy on body and fins, and often have yellowish lips. Both sexes carry about six vertical bars on the flanks. From *H.* "blue nyererei" it differs in male and female coloration, general appearance and by having a bigger mouth (longer and broader lower jaw relative to the head length). *H.* "Bwiru nyererei" was named after the place of its discovery, Bwiru Point, the peninsula between Speke Gulf and Mwanza Gulf entrance. Meanwhile we know it also from several other places along the southern Speke Gulf shoreline. It is absent from the offshore Speke Gulf islands. It lives in shallow water, between the surf zone rock boulders, and in deep rock pools, together with *H.* "zebra nyererei" and down to at least 2.5 m depth. *H.* "Bwiru nyererei" lives in sympatry also with *H.* "pink anal", *H.* "red rim anal", *H. nyererei* and *H.* "black and orange nyererei".

The remaining two species of this morphological group are anatomically and in coloration rather similar to each other and differ mainly in the lower jaw length/width ratio that is higher in ***Haplochromis* "red flank nyererei"**, and in the distribution of red colour on the body: In males of *H.* "red flank nyererei" red colour is most intensive on gill cover, chest and anterior flank while in ***Haplochromis* "all red nyererei"** it is most intensive on gill cover, chest, dorsal head surface and dorsum. In both forms the lower body half behind the red area, including the caudal peduncle, is greenish. The pelvic fin is black in the spinous, and red in the soft part. The dorsal fin is metallic blue with red lappets and streaks that are more prominent in "all red" than in "red flank". The anal fin is bright orange coloured in "all red" and red in "red flank". *H.* "all red nyererei" has weakly bicuspid teeth in the outer tooth rows. *H.* "red flank nyererei" can have unequally bicuspid teeth that are, for a species of the *H. nyererei* complex unusually closely spaced. Both forms have to be studied further to understand the relationship between them. *H.* "all red nyererei" is known only from the rock gardens of Gana Island northwest of Ukerewe were we found it in open waters among big rock boulders at depths between 3 and 7 m. A single individual of a very similar form has been collected at Ndurwa Point in the southern Speke Gulf. *H.* "red flank nyererei" is known only from Nansio Bay. At the small Nansio Island it lives in medium boulder size habitats between 1.5 and at least 5 m water depth. Both forms are not very abundant in their habitats. "All read" lives sympatrically with *H. cf. nyererei*, *H. cf.* "zebra nyererei" and *H.* "lemon fin nyererei". "Red flank" lives sympatrically with *H.* "zebra nyererei" and *H.* "Ukerewe nyererei".

Apart from the red *H. cf. nyererei*, a few other *H. nyererei* group species are known also from northern waters of Lake Victoria. A very beautiful species has recently been imported to the US and Europe under the misleading trade name *Haplochromis* "nyererei red", and has been introduced to hobbyists under the name ***Haplochromis* "crimson tide"** (DeMason 1996). Though of typical *H. nyererei* appearance it is very different from red *H. nyererei* as described by Witte-Maas and Witte (1985) and defined above. A better name, because describing a unique feature of the species, would be "red snout nyererei". Males have a light whitish grey dorsum, a dark greenish to black underside and caudal peduncle, and 6-7 black vertical bars on the flanks. The gill cover and the flanks behind the pectoral fins, between the light dorsum and the dark underside, are bright yellow to orange-red, interrupted by the vertical bars. As a peculiar feature the snout is bright orange-red, as if dipped into dye. Judging from my experience with it in aquaria, the species may remain rather small. Nothing is known about its life in nature. Considering its "body centre coloration" pattern I would postulate that it is a bottom oriented rather than a predominantly pelagic forager. A light blue coloured species of the *H. nyererei* complex with about eight narrow vertical

Ndurwa Point, the habitat of *H.* "red rim anal".

A male *H.* "red rim anal" (Ndurwa).

H. "red anal nyererei" at Vesi Is.

A male *H.* "all red nyererei" at Gana Island.

A male *H.* "Bwiru nyererei" from Bwiru.

A female *H.* "Bwiru nyererei" from Igombe Is.

A male *H.* "red flank nyererei" from Nansio Is.

bars on the flanks and a shape that vaguely reminds of *H.* "big blue" has many years ago appeared in the aquaria of European hobbyists (photos in Bleher in press). Details about its origin are not available, but most likely it had been sent out by exporters from Uganda or Kenya. A big, blueish species with steep dorsal head profile, that in general appearance resembles *H.* "big blue", has also been collected by staff of the Kenyan Fisheries Research Institute and was exhibited in the aquarium of the Ken-

The beautiful "rock garden" at Gana Island at noon time. Four different species from the *H. nyererei* complex are found here.

A male *H*. "crimson tide" in the aquarium.

yan Natural History Museum. A male of what might be the same species, was collected near Kisumu around 1989 (L. Kaufman pers. comm.), and was sent in a mixed shipment of Victorian cichlids to Germany (Seegers 1990). This patchy information indicates that the *H. nyererei* species complex has a lake wide distribution and that many more species are to be expected.

Large heads — the *Haplochromis* "deepwater" complex

This is a small complex of species, that inhabit the deeper parts of rocky littorals, or crevices and holes in shallower water. They feed on a variety of food types, ranging from zooplankton to epilithic sponges. None of the species is described. Anatomically the "Deepwaters" are very close to the species of the *H. nyererei*-complex, in particular to those of the "zebra nyererei group". Like those, most "Deepwaters" have a relatively long head and long lower jaws. The complex can be characterized by a combination of the following characters: straight to incurved dorsal head profile; unequally bicuspid to unicuspid, acutely pointed teeth in the outer tooth row, that are in large males rather coarse, with recurved crowns; 2 to 5 rows of inner teeth; a gap between the outer and the first inner tooth row; a lower jaw length of 40-42.4% of head length; a lower jaw length/width ratio of 1.4-1.9; a relatively narrow head with an interorbital width of 22.6-23.8% of head length; small deeply embedded chest scales, and a faint melanin pattern of 5 to 6 vertical bars between pectoral fin and caudal end of the dorsal fin. Most characteristics overlap considerably with those of the *H. nyererei*-complex and it appears plausible that the "Deepwaters" are indeed very close to the latter. Nevertheless, "Deepwaters" share a distinct appearance. Probably the best criteria to tell them apart from "Nyererei", are the melanin pattern, the large egg dummies, and the combination of a big, "heavy" head with a narrow interorbital width. Furthermore, in some "Deepwater" species the sensory pores of the lateral line system on the head are enlarged. They probably serve to locate prey in the dim-light environment of the "Deepwaters". Notwithstanding the close anatomical resemblance between "Deepwater" and "Nyererei" species, a considerable resemblance in male coloration between the species of the "Deepwater"-complex, *H. (Neochromis)* "velvet black" and *H. (Xystichromis)* "copper black" deserves mentioning (see photos).

Taxonomy within the *Haplochromis* "deepwater" complex is still problematic.

Currently I consider one species as rather widely distributed (the matrix species of the complex), while three others are known only from the Mwanza Gulf. The pattern of geographical distribution along the Mwanza Gulf is very similar to that observed among species of the *H.* "pseudonigricans"-complex (page 133): There is a consistently sympatric species pair in the southern Mwanza Gulf, made up of one blue and one yellow-red species, which from the central/northern Mwanza Gulf into the Speke Gulf is replaced by a black species. Like the "Pseudonigricans"-complex, the "Deepwater"-complex is absent from large parts of the Sengerema region with its very gently sloping shores.

***Haplochromis* "deepwater"** was the first species in this complex to be discovered by N. Bouton and myself in 1991. It is found at many moderately steep to steeply sloping shores in the central and northern Mwanza Gulf and has a scattered distribution in the Speke Gulf. Though its southernmost record, the Python Islands, are near to the northernmost records of *H.* "blue deepwater" and *H.* "yellow deepwater", it has never been found sympatric with any of these. The exclusive distribution and the correlation between geographical distribution and coloration, that resembles a similar correlation in the *H.* "pseudonigricans" complex (see below), suggest that *H.* "deepwater" and the two southern forms ("blue deepwater" and "yellow deepwater") are eco-geographical vicariants of one lineage.

Apart from the anal fin which can be wine red or black and carries large to very large yellow egg dummies, males of *H.* "deepwater" are entirely velvet black. A metallic iridescent silvery-blue band in the spiny part of the dorsal fin helps to tell *H.* "deepwater" apart from the sympatric *H. (Neochromis)* "velvet black" and *H. (Xystichromis)* "copper black" (that have, of course, very different dentition). Females are dark brown and resemble in coloration closely those of *H. (N.)* "velvet black". Male *H.* "deepwater" have a straight to slightly incurved dorsal head profile, that of females is frequently slightly decurved. Though rather variable in this respect, *H.* "deepwater" have strong jaws and somewhat thickened lips. Adult males in many populations are easily recognized by their body shape: body depth decreases rapidly from slightly behind the head to the caudal peduncle, making it that the head appears particularly heavy. Among all known *Mbipi*, this species has the most prominent sensory pores on lachrymal, preoperculum and dentary bones.

H. "deepwater" lives at moderately steep and steep rocky shores and at most places at water depths from 2 to at least 10 m. Like many other deep water dwelling *Mbipi*, it stays offshore at moderately steep shores, but can be found among inshore rock boulders and in deep rock pools at less than 2 m depth, where the shore drops off steeply. The microhabitat choice, deep water versus inshore rocky crevices, may depend also on the presence or absence of *H.* "zebra nyererei" in the crevices. Where the latter is abundant, *H.* "deepwater" does not live in inshore crevices. The well studied population that inhabits the Python Islands feeds predominantly on insect larvae, epilithic sponges, ostracods, plankton and the detritus layer covering the rocks at greater depths (Bouton et al. submitted, pers. obs.). At Hippo Island, we found *H.* "deepwater" feeding also on small snails.

It is unclear, how far the species´ absence from many places in the Speke Gulf is due to ecological factors. It is there absent from many gently sloping shores and islands but also from several steeply sloping large boulder habitats, like Ndurwa Point, Ruti and Vesi Islands, and one of its records from the northern Speke Gulf (Zue Island) is from an island with gentle slope and small boulders.

***Haplochromis* "yellow deepwater"** is known only from the southern Mwanza Gulf, where it has been recorded at all sampled stations of rocky habitat south of, and including Luanso Island. Males are yellowish grey to yellow with a reddish head, dorsum and dorsal fin. Characteristic is a metallic iridescent area on each scale, giving the fish a silvery "pelagic" appearance. The caudal fin is transparent with many red-brown dots and streaks. The faint reddish anal fin carries several, often large, pale yellow egg dummies. Females are greyish. *H.* "yellow deepwater" has usually a straight dorsal head profile, and a bigger mouth (longer and broader lower jaw) than its sympatric sibling, *H.* "blue deepwater". It lives slightly offshore, beyond 2 m water depth, and is absent from the inshore rock pools and crevices that are inhabited by *H.* "blue deepwater". *H.* "yellow deepwater" is usually the most abundant haplochromine in the deeper parts of the rocky habitat in the southern Mwanza Gulf. It occupies there a niche that is occupied by *H. nyererei* in the northern Mwanza Gulf. Of two individuals we checked stomachs. One was empty, the other one contained only unidentifiable, mashed material that may have been zooplankton. At most of its record localities *H.* "yellow deepwater" coexists with *Haplochromis* "blue deepwater". However, at the southern most rock shore that we sampled (Buyago rocks in the Smith Sound), we found only the yellow species.

***Haplochromis* "blue deepwater"** is morphologically very similar to *H.* "yellow deepwater", though adults are usually somewhat deeper bodied, and give a generally more robust impression. Their dentition is more typical for a benthic feeder, with more inner tooth rows (see table 3). Males are metallic blue all over and in contrast to the other species in this complex, often lack any red pigment in the fins. Their egg dummies are smaller than those of *H.* "yellow deepwater". Females of these two species can hardly be told apart. The distribution of *H.* "blue deepwater" resembles that of *H.* "yellow deepwater", though it is absent from the Smith Sound in the south and extends slightly further north to Mashoro Bay and the northern Luanso Bay. In contrast to its yellow sibling, *H.* "blue deepwater" lives inshore, in crevices and rock pools in shallow water. It is hardly ever found at depths beyond 2 m or more than a few metres off shore. It therefore occupies in the southern Mwanza Gulf a niche very similar to that occupied by *H.* "zebra nyererei" in the central and northern Mwanza Gulf and Speke Gulf. At an islet near Python Islands in the central Mwanza Gulf, we did not find *H.* "zebra nyererei" in rocky crevices, as on Python Islands proper, but a population of cichlids similar to *H.* "blue deepwater". If these fishes prove to be *H.* "blue deepwater", this species would live at least parapatrically with *H.* "deepwater", the latter inhabiting greater depth. Information about the diet of *H.* "blue deepwater" is not yet available, however, the combination of morphology and microhabitat suggests that the species lives mainly on insect larvae and animalous epilithic *Aufwuchs*.

A so-called high energy shore at the south-east corner of Bwiru Island.

A male *H*. "deepwater" from Python Island.

A female *H*. "deepwater" from Python Island.

The least known species in the "Deepwater complex" is ***Haplochromis* "slender deepwater"**. To date it has been recorded only from Hippo Island in the northern Mwanza Gulf and just a couple of individuals have been collected. All were caught at the south-west corner of the island at depths between 6 and 9 m. They live sympatrically and syntopically with *H.* "deepwater", from which they differ conspicuously by a shorter head, more elongate body and more pointed snout. Also the eyes are bigger. Since no brightly coloured male was among the collected individuals, male breeding coloration is not yet known. Available males were dull dark brown with a faint reddish sheen on the back and a reddish anal fin with orange coloured egg dummies.

The *Haplochromis* "pseudonigricans" complex

This is a complex of anatomically rather generalized *Mbipi* species, that are anatomically not far removed from unspecialized "*Astatotilapia*"-like cichlids. Despite this, it is my experience that most of its members, can on first glance be recognized as such. It is much more difficult, however, to give a definition of the species complex. It could be described as taking a position between the *Neochromis*-complex of algae scrapers and generalized insectivorous haplochromines (e.g. *Astatotilapia nubila*). In many measurements the *H.* "pseudonigricans"-complex broadly overlaps also with the *H. nyererei*-complex, though the species of the two lineages are of quite different general appearance.

Some "Pseudonigricans" species have a steep, decurved dorsal head profile like *Neochromis* species, others have a straight dorsal head profile and in most species it is intermediate. It is usually not as shallow as that of many *H. nyererei*-complex species, and only very rarely incurved. The head is usually narrower (21-26.4% of head length) than that of most *Nyererei* species, and the eyes are bigger than in most other *Mbipi* (25.1-30.2% of head length). The lower jaw is not as broad as in *Neochromis* species (length/width ratio 1.4 to 1.9, in one exception 1.2), and usually shorter than in *Nyererei* species (36.9 to 39.1% of head length, in two species about 41%). The inner teeth are arranged in fewer (2-4), and less broad bands than in *Neochromis*. The outer teeth are not contiguously set, but the interspaces between them are usually relatively small (not as wide as the width of the tooth neck). The shape of the outer teeth is less scraper-like than in most *Neochromis* (unequally bicuspid to unicuspid, rarely subequally bicuspid). Nevertheless, they are usually moveably implanted even in adult males, and not as coarse as in most "Nyerereis" and "Deepwaters". The scales on the chest are small and deeply embedded. The melanin pattern consists of 4 to 6 vertical bars between pectoral fin and caudal end of the dorsal fin, which are broader, and often less distinct than those in *Nyererei* species. They are frequently


A male *H.* "blue deepwater" (Luanso Bay).


A female *H.* "blue deepwater".


A male *H.* "yellow deepwater" (Luanso Bay).


A male *H.* "slender deepwater" from Hippo Is.

broader than the interspaces between them, a situation that is very rare in *Nyererei* species. Females of most "Pseudonigricans" species are considerably much smaller than males, and frequently have more scraper-like dentition, with closer set bicuspid teeth.

Overlap with other species complexes of *Mbipi* is considerable in most of the individual characters that I measured, but clustering various *Mbipi* species based on the combination of these characters, produced a tree, in which 11 of 13 "Pseudonigricans-species" clustered together. This confirms the subjective impression, that we are dealing with a group of species that have more in common with each other, than with species of other groups.

Also ecologically the species of the *H.* "pseudonigricans"-complex occupy on average a position between specialized algae scrapers, more generalized insectivores and planktivores. Most species are either epilithic *Aufwuchs*-feeders that feed predominantly on animal components of the *Aufwuchs*, and to lesser extends on plankton and epilithic algae, or plankton feeders that forage, similar to *H. nyererei*, in the currents that prevail at the edge of rocky reefs, but consume also some *Aufwuchs*. Their feeding behaviour consists mainly of snapping, picking and scraping (described by Seehausen et al. in press [a]). While the majority of the *Neochromis*, and some *Nyererei* species inhabit shallow waters over gentle slopes, all known "Pseudonigricans"-complex species live either somewhat offshore at greater depths, or inshore at very steep slopes. In this respect they resemble species of the "Deepwater" complex, but it is more uncommon to find them in rock holes.

***Haplochromis* "black pseudonigricans"** was the first form of the species complex to be discovered (Witte et al. 1992), and is taxonomically one of the most difficult ones of all. We know it only from a geographically very restricted region, the rocks at the southern Nyegezi bay entrance and nearbye islets, collectively referred to as the Nyegezi rocks (Mwanza Gulf). This is an area that harbours an exceptionally high diversity within the *Haplochromis* "pseudonigricans"-complex. We know from there at least five sympatric forms, while the highest number elsewhere is three, and over large areas only one or two forms can be found at any one place. While some of the forms at Nyegezi rocks belong to more widely distributed species (*H.* "black and yellow pseudonigricans", *H.* "long snout pseudonigricans", *H.* "pseudoblue"), two have never been seen anywhere else. One of them is *H.* "large eye pseudonigricans", the other one is *H.* "black pseudonigricans". The situation is particularly difficult, since we found intermediate phenotypes like large eyed "black and yellow" pseudonigricans", that suggest that occasional gene flow occurs among the narrowly endemic forms and *H.* "black and yellow pseudonigricans". Nevertheless, material and field notes, collected as early as 1978 by Els Witte-Maas and Frans Witte, indicate that these three forms have been persisting at Nyegezi rocks over quite some time. Conform with the species recognition criteria outlined in the chapter about taxonomy, I therefore consider these forms different species. Research on mate choice and heritability of anatomical and coloration differences should proof this right or wrong.

Males of *H.* "black pseudonigricans" can on first glance be confused with *H. (Neochromis)* "velvet black". They have metallic blue-black to velvet black, flanks, and at some islets some purplish sheen on the dorsum. The anal fin is reddish to grey transparent and carries small yellow egg dummies. The caudal fin is grey with a red flush to red. The dorsal fin carries a red rim and frequently red streaks in the soft part, though the red is not as prominent as in *H.* "blue pseudonigricans" and *H.* "large eye pseudonigricans". We consider a form that is entirely grey with a weak metallic blue sheen on the flanks and transparent fins as a morph of *H.* "black pseudonigricans", because it does not differ anatomically from the blue-black form. *H.* "black pseudonigricans" has a peculiar dorsal head profile.

It is relatively steep and straight, but with a small concavity, above the eye. As a consequence, the premaxillary pedicels appear prominent, giving the snout a tapering appearance. It is with difficulty that females of the five sympatric species from the Nyegezi rocks can be assigned to the males. However, also females exist in five different forms. The type of females that I believe to belong to the *H.* "black pseudonigricans" males, has a similar dorsal head profile (straight or "tapering mouth") and exhibits a blueish sheen on the flanks.

The habitat of *H.* "black pseudonigricans" is characterized by steeply sloping, almost vertically dropping huge rock boulders. Here it lives immediately inshore between 1 and at least 4 m water depth. We never caught it in nets that were set a few metres further away from the shore.

***Haplochromis* "large eye pseudonigricans"** differs from the foregoing species anatomically and in coloration. Also from all other members of the "Pseudonigricans" complex it differs by its small lower jaw length/width ratio that resembles that found in *Neochromis* species. With the latter it shares furthermore the steep and slightly decurved dorsal head profile. Its very large eyes are comparable in size only to those of *H. (Neochromis)* "large eye nigricans" and *H. (Xystichromis)* "large eye black" (table 3), and its large egg dummies to those of "Deepwater" complex species. Males have grey-blue to bright metallic blue flanks, and on the dorsum frequently a reddish flush. The dorsal fin is blue in most of the spinous and bright red in most of the soft part. The colour border is often sharp and runs obliquely across the fin (see photo). This dorsal fin coloration is basically the same as that found in many individuals of *H.* "blue pseudonigricans". Like in the latter, caudal and anal fin of "large eye pseudonigricans" are bright red. Different are the egg dummies. While orange coloured in *H.* "blue pseudonigricans", they are yolk yellow in *H.* "large eye pseudonigricans". Moreover they are bigger and commonly two or more flow into each other. Confluent egg dummies are a rare feature among rock-dwelling Lake Victoria cichlids, and known only from one other deep water dwelling species (*H. (Ptyochromis)* "striped sheller"). "Large eye pseudonigricans" has never been caught by angling rod, and seems to live slightly deeper and/or more offshore than *H.* "black pseudonigricans". Judging from its morphology it probably feeds upon animal *Aufwuchs* from the rocks. I consider this species closely related to *H.* "blue pseudonigricans". It might be derived from a population of that southern species, that met at Nyegezi rocks with another, (northern) ecologically similar species of the complex (*H.* "black and yellow pseudonigricans"), and as a result of competitive interaction with this, was pushed into a different ecological niche. However, this speculative hypothesis may prove difficult to test.

The Nyegezi rocks are a meeting point between the southern and the northern group of the "Pseudonigricans" complex. From their fauna one can easily move on via *H.* "black and yellow pseudonigricans" to the northern group, and via *H.* "large eye pseudonigricans" to the southern one. Interestingly the "Pseudonigricans" species of the Mwanza Gulf display a geographical distribution pattern in relation to male coloration that is very similar to the one described for the "Deepwater" complex (see page 126). The southern and central Mwanza Gulf is inhabited by two sibling species, one red (*H.* "red pseudonigricans"), the other one blue (*H.* "blue pseudonigricans"), while black male coloration dominates at the steeply sloping shores further north.

Most widely distributed in the south is ***Haplochromis* "blue pseudonigricans"**. It is currently known from each sampled station in the southern Mwanza Gulf between Marumbi Island and Python Islands. We did not find it, however, in the Smith Sound, the south-western extension of the Mwanza Gulf. North of Python Island it is restricted to the western shore of the Mwanza Gulf, where it is known from Ngoma Peninsula, Kissenda Bay and Hippo Island. This is a conspicuously coloured species. Males are bright metallic iridescent sky blue all over,

Nyegezi Rocks, habitat of several Pseudonigricans complex species.

A male *H*. "black pseudonigricans" (Ngoma).

H. "large eye pseudonigricans" (Ngoma Point).

A male *H*. "blue pseudonigricans".

A male *H*. "blue pseudonigricans" from Python Is.

with a bright blood red anal fin, caudal fin and soft dorsal fin. The red area in the dorsal fin, often dissolved into streaks on the fin membranes, is usually sharply demarcated against the metallic blue anterior parts of the fin. The egg dummies on the anal fin are usually orange. At one place in the central Mwanza Gulf (Matumbi Island) we found a rare colour morph with a red dorsum, that was otherwise identical with the blue males. Females are light yellowish brown with a silvery metallic sheen ("pelagic" appearance). *H.* "blue pseudonigricans" is one of the deeper bodied species in the complex. Its dorsal head profile is straight, often slightly concave. Most populations, particularly in the south, have very regularly arranged, small and fine teeth that are usually bicuspid. In the southern parts of its range, populations of *H.* "blue pseudonigricans" from different islands do not, or hardly differ from each other. Towards the north, however, more distinct morphological differences become apparent between populations. So does the population of Kissenda Island (northern Mwanza Gulf) have a significantly longer lower jaw than other populations, and females are darker brownish.

South of Python Islands, *H.* "blue pseudonigricans" lives at moderately to steeply sloping shores. Its relative to the Mwanza Gulf asymmetric geographical distribution north of Python Islands correlates with differences in the rocky habitat between the steeply sloping eastern shore and the moderately steep western shore of the northern Mwanza Gulf. Thus it seems in the northern Mwanza Gulf to avoid steep slopes, which are inhabited there by *H.* "black and yellow pseudonigricans". At moderately steep slopes adult *H.* "blue pseudonigricans" usually stay several metres offshore, at steep slopes they can be caught immediately inshore. The species lives at depths from 1 (rarely) to at least 8 m, and seems to frequently forage in the open water column above, or next to the rocks.

Of five individuals that we checked, two had empty stomachs, one had eaten predominantly zooplankton, one caddis fly larvae (Trichoptera) and one may fly larvae (Ephemeroptera). None had any bottom

A territorial male *Haplochromis* "red pseudonigricans" in the aquarium.

material or epilithic algae in its stomach. Thus this species seems to forage pelagically in the water column and by picking up insect larvae from the rocks without scraping from the *Aufwuchs.* In feeding experiments in aquaria, it behaved respectively and different from *H.* "black and yellow pseudonigricans" that used to scrape *Aufwuchs* (unpublished data). In parts of the geographical range of *H.* "blue pseudonigricans", large zooplankton (*Daphnia*) can be very abundant. While it is south of Python Islands the most abundant haplochromine in deeper parts of the rocky habitats, *H.* "blue pseudonigricans" is less abundant in the north-western Mwanza Gulf and very rare at Hippo Island.

From Python Islands southwards, *H.* "blue pseudonigricans" lives sympatrically with an anatomically extremely similar, but dramatically differently coloured species: *H.* "red pseudonigricans". In the northern part of its range, it also lives in sympatry with *H.* "pseudoblue", *H.* "long snout pseudonigricans" and *H.* "yellow chin pseudonigricans".

***Haplochromis* "red pseudonigricans"** and *H.* "blue pseudonigricans" appear to be sibling species. Like the blue species, we found also the red one at each sampled place in the southern and central Mwanza Gulf. However, we found it also in the Smith Sound (Buyago rocks), while it does not reach as far north as the blue one does. This distribution pattern resembles that of the yellow and blue sibling species of the "Deepwater" complex in astonishing detail (see page 126).

Between Marumbi Island and the Luanso Bay the two species are caught in approximately equal frequencies. At Python Islands and at Ngoma rocks, the northernmost records of *H.* "red pseudonigricans", this species is much less abundant than the blue one. In fact it has not been caught there before 1995 in spite of extensive sampling. Males of *H.* "red pseudonigricans" are bright blood red on the anterior flanks, head and belly. The posterior third of the flanks, and the caudal peduncle are yellowish to greenish. In less intensively coloured males the red is restricted to the lower chest. It is readily possible to tell this species apart from the reddish morph of *H.* "blue pseudonigricans". The red in *H.* "red pseudonigricans" is ventrally oriented and does not reach the upper dorsum. In contrast, the red in the red morph of its sibling species is dorsally oriented, and in fact restricted to the dorsum and the dorsal fin. If the red on the flanks of *H.* "red pseudonigricans" males entirely fades away, they are still recognizable by the absence, or but faint expression of red in the fins. If faintly present, this red in the fins is more wine-red, while it is blood-red in *H.* "blue pseudonigricans". Moreover, *H.* "red pseudonigricans" has a red flush on the gill cover, and its egg dummies are usually smaller than in *H.* "blue pseudonigricans". Some males have a part of the pelvic fins red. Females of "red pseudonigricans" are usually more brassy, and less silvery in colour than those of "blue pseudonigricans".

Ecologically *H.* "red pseudonigricans" differs slightly from *H.* "blue pseudonigricans". It lives more inshore, has rarely been caught in nets set some metres away from the shore or in open water and never at depths beyond 4 m. As far as the limited data allow to judge, the more littoral orientation is reflected in the feeding habits of "red pseudonigricans". Of three individuals that we checked, one had the stomach empty, one had eaten only insect larvae (of may and caddis flies), and one exclusively small snails. The teeth of "red pseudonigricans" tend to develop a larger flange, thus a more scraper-like shape, suitable to take up food items from a rock surface. Finally, the female coloration does indicate that this species lives more inshore and bottom oriented than its blue sibling.

***Haplochromis* "black and yellow pseudonigricans"** is known exclusively from the steeply sloping rock shores of the north-eastern Mwanza Gulf were it is rather abundant at the mainland as well as at islands. Its southernmost record is from the Nyegezi rocks, where it overlaps with a number of other species (see above). It is morphologically (Table 3) very close to the large group of populations inhabiting islands in the Speke Gulf and open lake, which I consider populations of a single species, *H.* "yellow chin pseudonigricans". The major argument, to consider the north-eastern Mwanza Gulf populations specifically distinct, is a different female coloration (see below). "Black and yellow pseudonigricans" has nowhere been found sympatrically with "yellow chins", but the Hippo Island population of the latter is separated from the Gabalema Island population of "black and yellow pseudonigricans" by less than 2 km of open water.

Males are entirely deep black with dorsal fin lappets that are yellow in the spinous part and orange to red in the soft part, a relatively broad red caudal fin edge, and a bright yellow, sometimes orange anal fin with small yellow egg dummies. This coloration resembles in astonishing detail the body outline coloration of some species in the *H. nyererei* complex (see page 113). Females of *H.* "black and yellow pseudonigricans" are brownish with five broad vertical bars on the flanks. They have a rather steep, usually slightly decurved dorsal head profile, and lack the bright yellow chin and throat that is characteristic for the females of *H.* "yellow chin pseudonigricans". Females and subadult males of *H.* "black and yellow pseudonigricans" can be told apart from those of *H.* "blue pseudonigricans" by the lack of the silvery iridescence on the flanks (no "pelagic" appearance), and by the dorsal head profile. From those of *H.* "large eye pseudonigricans" they differ in eye size.

With the decurved dorsal head profile and relatively broad lower jaw, *H.* "black and yellow pseudonigricans" reminds of some epilithic algae scrapers of the *Neochromis* lineage. Also otherwise its morphology is, more than that of *H.* "blue pseudonigricans" and *H.* "red pseudonigricans", that of a fish that removes firmly attached food items from a rock surface. So are the outer teeth stronger. The well studied population at Anchor Island feeds predominantly on insect larvae, epilithic *Aufwuchs* (filamentous blue-green algae, moss animals), prawns, detritus and fish (Bouton et al. submitted) and employs mainly picking, scraping and snapping as feeding techniques (Seehausen et al. in press [a]).

More than any other known species of the "Pseudonigricans" complex, "black and yellow pseudonigricans" is restricted to habitats with large, very steeply sloping boulders, where it lives immediately inshore between 0.5 m and at least 5 m water depth and in crevices between the shore rocks. It is usually found sympatrically with *H. (Neochromis)* "velvet black". These two species are the numerically dominant *Mbipi* in most of the "steep-slope communities" of the north-eastern Mwanza Gulf. If the hypothesis is correct that I formulated on page 110 to explain the function of body outline coloration, "black and yellow pseudonigricans" might resemble some *Nyererei* species in a sexually dimorphic ecology, with males defending territories on the rock bottom and females living so to speak above the heads of the males. The low water transparency in the Mwanza Gulf prevented underwater observations so far. Females of "black and yellow pseudonigricans", however, in contrast to those of *Nyererei* species with body outline coloration, do not appear to be shoaling. Nevertheless, by Scuba I observed at Miandere Island in the open lake a population of *H.* "yellow chin pseudonigricans" with body outline coloration, the behaviour of which is indeed conform to the hypothesis.

Under the name ***Haplochromis* "yellow chin pseudonigricans"** I unite a large number of phenotypically similar, but geographically well isolated populations. They mostly inhabit offshore islands in the open lake and in the Speke Gulf, but are largely absent from mainland shores. Some share with *H.* "black and yellow pseudonigricans" the yellow anal fin of the males, in others it is red and several populations are polymorphic in this respect. The small egg dummies are yellow to orange-red. The males from Miandere Island in the west of our survey area have a pale, yellowish white anal fin with or-

Luanso Island, habitat of *H.* "blue pseudonigricans" and *H.* "red pseudonigricans".

H. "red pseudonigricans" from Shadi Rocks.

H. "red pseudonigricans" from Ngoma Point.

H. "black & yellow pseudonigricans" (Ngoma).

A peppered *H.* "black & yellow pseudonigricans".

ange-red egg dummies. The body coloration of males is blue-green to green-black, at some islands almost black. Females are yellowish brown, similar to those of *H.* "black and yellow pseudonigricans" but are characterized by a bright yellow chin, brachyostegal membranes and throat. Like *H.* "black and yellow pseudonigricans" also these populations lack the metallic iridescence that gives species like *H.* "blue pseudonigricans" and *H.* "pseudoblue" their "pelagic" appearance.

The dorsal head profile of *H.* "yellow chin pseudonigricans" is less steep than that of *H.* "black and yellow pseudonigricans" and is often straight, rather than decurved. Its lower jaw is usually longer. These anatomical differences suggest that "yellow chin" is less substrate oriented in its feeding. Our

A male *H*. "yellow chin pseudonigricans" from Miandere Island.

H. " yellow chin pseudonigricans" (Miandere).

H. "yellow chin pseudonigricans", a female.

A male *H*. "orange pseudonigricans" (Sozihe).

A female *H*. "orange pseudonigricans" (Sozihe).

data on diet corroborate this: Of three males from Makobe Island, the stomachs of which we checked, one had eaten predominantly zooplankton, another one zooplankton, may fly larvae, and filamentous blue-green algae, and the third one filamentous blue-greens, green algae, diatoms, and to a lesser extent zooplankton and insect larvae. At Ruti Island, I observed females moving in shoals, partly mixed with *H. nyererei*, and foraging on plankton. At Miandere Island, I observed similar mixed shoals with *H.* "orange dorsal nyererei". Usually *H.* "yellow chin pseudonigricans" lives slightly offshore and at depths beyond 3 m. At steeply sloping islands, however, it can be observed more inshore, though rarely at depths of less than 2 m. At the gently sloping Makobe and Zue Islands adults are restricted to the more offshore regions and depths between 4 and 8 m, though individuals are now and then seen in shallower water. Subadults have been caught at Zue Island at about 1 m depth. At Hippo Island the species goes at least as deep as 10 m. At the gently sloping islands, *H.* "yellow chin pseudonigricans" occurs in low or moderate densities, while it can be rather abundant at some steep islands (e.g. in the Vesi Archipelago). The distribution pattern of this species is very peculiar. It is widely distributed, inhabiting every offshore island in the Speke Gulf and those that have been sampled in the Sengerema region (apart from the very gently sloping ones), but occurs only very rarely at mainland rock shores. At the mainland on both sides of the Speke Gulf we found very different species of the "Pseudonigricans" complex (compare maps).

Considering the extreme patchiness of the habitat of *H.* "yellow chin pseudonigricans", and its wide distribution, geographical variation is to be expected. Its populations are isolated from each other by deep open water over large geographical distances. They differ from each other mainly in male coloration and attained maximum size. The differences in coloration are largely confined to the darkness of the flanks and to the anal fin colour, and a correlation between habitat type and male coloration exists. The red anal fin morph dominates, or is the exclusive one at places with more gently sloping shores and smaller rock boulders, the yellow one at places with steeper slopes and big boulders. The body coloration is darker, and changes from blue to green-black, the steeper the rocky slopes in the habitat are. It resembles at the very steep Ruti Island the coloration of *H.* "black and yellow pseudonigricans". Distinct from all other known populations is the population from Miandere Island with its aberrant yellowish-white anal fin and a small maximum size of about 8 cm SL. Its aberrant characters may have evolved in response to coexistence with two ecologically similar species of the *Nyererei* complex: *H.* "orange dorsal nyererei" and *H.* "small mouth nyererei". The latter species resembles in coloration closely the yellow anal morph of *H.* "yellow chin pseudonigricans".

I consider *H.* "yellow chin pseudonigricans" the matrix species of the "Pseudonigricans" complex. The correlation between habitat characteristics and male coloration among its populations, together with the distribution pattern of *H.* "black and yellow pseudonigricans", being restricted to a region with steep shores, strongly suggest convergent or parallel evolution of male coloration in response to environmental light conditions. The mutually exclusive distributions of "yellow chins" and *H.* "black and yellow pseudonigricans" in the northern Mwanza Gulf, suggest that the two forms, though now different in more than just male coloration, have evolved from one ancestral stock as eco-geographically vicariating species. More work is needed, in particular about the evolution of male coloration, before these interesting patterns can be disentangled.

Very interesting in this respect is also a species that is so far known only from the eastern most island that we sampled, ***Haplochromis* "orange pseudonigricans"** from Sozihe Islands in the Speke Gulf. Anatomically it is close to the populations of the "yellow chin"/"black and yellow pseudonigricans" lineage. However, it is very distinct in male coloration, and females resemble those of the *H.* "scraper pseudonigricans" lineage (see below). When we spotted these fishes for the first time in our nets, we thought for a moment of *H. nyererei*. Males have the *H. nyererei*-colour pattern with a bright orange dorsum, dark vertical bars, and a blueish to greenish lower half of the body and caudal peduncle (compare with the photo of *H. nyererei* from Senga Point). Lappets and soft part of the dorsal fin, the caudal fin, and the anal fin are bright orange. However, the vertical bars on the flanks are fewer and broader than in *H. nyererei,* which is in females particularly apparent. Females bear a high-contrast melanin pattern with about six broad vertical bars. This is rare among "Pseudonigricans" species, and is found otherwise only in females of the *H.* "scraper pseudonigricans"-group. Females of "orange pseudonigricans" lack a yellow chin. From *H. nyererei*, that does not occur at Sozihe Islands, "orange pseudonigricans" differs anatomically.

The habitat of *H.* "orange pseudonigricans" is variable. It lives at Sozihe Islands at places with gentle, moderate and steep slopes, and over small to very big boulders. Females and subadult males are found in shallow waters of just 1 m depth as well as at greater depths. Reproductively active adult males in breeding dress are restricted to depths beyond 2.5 m and are abundant in waters of 5 to at least 7 m depth. In the greater depths they are, together with *H.* cf. "blue nyererei", the dominant haplochromine species at Sozihe Islands.

Males with coloration reminiscent of that of *H.* "orange pseudonigricans" occasionally occur within the geographical range of *H.* "black and yellow pseudonigricans" (Gabalema Islands, Anchor Island). It is likely that these are rare phenotypes of the "black and yellow pseudonigricans" populations. Their occurrence, however, may indicate a certain disposition to orange male coloration and hint at possible phylogenetic relationships.

The mainland shores of the Speke Gulf and of the open lake are home to a number of "Pseudonigricans" complex species that share a relatively steep dorsal head profile, bicuspid outer teeth, an increased number of inner tooth rows and a rather inconspicuous blueish-grey to black male coloration. For as yet not understood reasons, non of the islands in the Speke Gulf is inhabited by such fishes and thus they rarely live in sympatry with "yellow chins". ***Haplochromis*** **"scraper pseudonigricans"** is known from all rocky peninsulas along the southern Speke Gulf shore, between the Bwiru peninsula at the corner to the Mwanza Gulf, and Senga Point. This is anatomically the most extreme scraper type within the *H.* "pseudonigricans"-complex. Its dentition resembles that of the least specialized *Neochromis* species with subequally bicuspid outer teeth and up to 5 rows of inner teeth. The outer teeth, however, are rather widely spaced, and the gap between outer and inner teeth is wide. The dorsal head profile is decurved and rather steep, the snout has often the tapering appearance that I described above for *H.* "black pseudonigricans", the lower jaw is not as broad as in *H.* "large eye pseudonigricans". Males are light blue with red dorsal fin lappets at the places with the clearest water. They become black towards the interior of the Speke Gulf. In contrast to most other "Pseudonigricans" species, this one has a grey to black anal fin without any red. The small egg dummies are yellow. The caudal fin is grey to black with a small red upper corner. At some places we found alongside the blue-black type a second, yellowish colour morph with reddish-brown dorsum. Though we caught already about 25 males of this in 1995 discovered species, we found only one female yet. It has a much narrower head than the males, and shows a high-contrast melanin pattern, consisting of five broad vertical bars on brassy ground, similar to the pattern displayed by females of *H.* "orange pseudonigricans".

H. "scraper pseudonigricans" inhabits the steeply sloping large boulder shore at Bwiru Point, the moderately steep

Steep shores with large boulders are the habitat of *Haplochromis* "scraper pseudonigricans".

slope of Igombe Island with smaller boulders, and intermediate habitats at Ndurwa and Senga Points. It seems to be absent from gently sloping, small boulder habitats at Ndurwa Point. *H.* "scraper pseudonigricans" lives at water depths between 1.5 and 6 m, and usually not directly inshore. Its diet is diverse. Of three individuals that we checked, one had eaten almost exclusively filamentous green algae, the second one zooplankton and plant material and the third one aquatic mites (*Sperchon*) and caddis fly larvae (Trichoptera). The change in male coloration that is observed among populations from west to east, is accompanied by a change in dentition. Eastern populations have a less typical scraper dentition, with unequally bicuspid outer teeth and fewer inner tooth rows, possibly reflecting different feeding habits in habitats in which algae growth is inhibited by less transparent water.

H. "scraper pseudonigricans" lives sympatrically with *H.* "yellow chin pseudonigricans" at Bwiru Point. However, the latter is very rare there. It furthermore lives in sympatry with several algae scrapers of the *Neochromis* and *Xystichromis* lineages (*H. (N.) nigricans*, *H. (N.)* "giant scraper", *H. (N.)* "velvet black", *H. (N.)* "unicuspid scraper", *H. (X.)* "copper black", *H. (X.)* "large eye black"). At most places *H.* "scraper pseudonigricans" is much less abundant than some *Neochromis* and *Xystichromis*. However, at Senga Point, a place with low haplochromine densities in deeper waters, this species is numerically dominant.

A form that is very similar to *H.* "scraper pseudonigricans" inhabits the northern mainland (Ukerewe) shores of the Speke Gulf. From the southern species it differs slightly in body shape, male coloration, and quite considerably in eye size. I therefore consider ***Haplochromis* "Ukerewe pseudonigricans"** specifically distinct. It is currently known from the steep eastern part of the Ukerewe shore between Namatembi Island and Nansio Bay, as well as from Bwiru Island. Males are light blue on the flanks. The dorsal fin is grey-blue with orange to red lappets. The edge of the caudal fin is red or orange on its entire length and the anal fin is usually faint yellow with small egg dummies.

The dorsal head profile is often less steep than in "scraper pseudonigricans" and the mouth opens to above rather than horizontally (slightly prognathous rather than isognathous snout outline). Finally, the eyes are considerably smaller. We found "Ukerewe pseudonigricans" between 2.5 and 5 m depth at moderate and steep slopes. Its dentition is less scraper-like than that of *H.* "scraper pseudonigricans". In the species rich and densely populated communities at Nansio and Bwiru islands it is very rare, while it is one of the commoner species in the species poor low density community at Namatembi Island (compare with "scraper pseudonigricans" at Senga Point). It lives in parts of its range sympatrically with *H.* "black Ukerewe" as another member of the "Pseudonigricans" complex.

A third species in the "scraper pseudonigricans" group is ***Haplochromis*** **"Gana pseudonigricans"** from Gana Island northwest of Ukerewe. This is a very short-headed species with a rather elongated body, and 5 broad dark vertical bars on flanks. The flanks are reddish on the upper half, yellow in the middle and yellow-green ventrally. The dorsal fin is grey or grey with red streaks and has orange to red lappets. Caudal and anal fin are largely orange to red. The steep dorsal head profile of adult males, combined with the elongated body, can be reminiscent of the condition in oral shelling snail eaters. However, the dentition with mostly bicuspid teeth is that of an insect eater. At Gana Island we observed this species in water of about 4 to 6 m depth in a huge rock garden, composed of very big boulders. It lives in sympatry with *H.* "black Ukerewe".

Haplochromis **"black Ukerewe"** is a long snouted black species with an elongated

H. "scraper pseudonigricans" (Bwiru Point).

A female *H*. "scraper pseudonigricans" (Bwiru).

H. "Ukerewe pseudonigricans".

A male *H*. "Gana pseudonigricans".

body that is known from several places in the Ukerewe region. The different populations hardly differ in coloration though they differ somewhat in other characters, e.g. body depth and lower jaw length. Males are dark grey with 4-5 broad vertical bars, to entirely black. Black is also the dorsal fin that has red lappets, while caudal and anal fin are in their proximal half greyish, in their distal half red. Females are brassy yellowish. *H.* "black Ukerewe" lives at moderately steep shores as well as in the rock gardens of Gana Island. We found it at water depths ranging from 2 to 6 m. Jaw anatomy and dentition suggest that *H.* "black Ukerewe" preys upon insect larvae and/or zooplankton.

Two species have longer lower jaws than all other "Pseudonigricans" species, and resemble in this respect the species of the "Deepwater" complex. Nevertheless, their overall appearance is more that of "Pseudonigricans" species and I tentatively include them in this species complex. ***Haplochromis*** **"long snout pseudonigricans"** is currently known from two places on opposing shores of the northern Mwanza Gulf: Nyegezi rocks at the east shore and Kissenda Island at the west shore. The species is readily distinguished from other members of the species complex by its long and acutely pointed snout and therefore shallow dorsal head profile in both sexes. Its dentition is of "Pseudonigricans" type. Males are dark blue to blue-black with dark red in the anal and caudal fins, a few dark red streaks in the soft dorsal fin, and dark red dorsal fin lappets. Females are brownish with a metallic greenish flush on the flanks. *H.* "long snout pseudonigricans" lives at Kissenda Island in sympatry with a population of *H.* "blue pseudonigricans" that has also exceptionally long jaws, but otherwise differs from *H.* "long snout pseudonigricans" anatomically and in male coloration. Male flank coloration of "blue pseudonigricans" is a lighter blue, fin coloration a lighter red than in "long snout pseudonigricans". The dorsal fin of "blue pseudonigricans" is bright red between the soft rays. The outer teeth of adults are usually bicuspid in both species but much more outworn in "long snouts" than in most "blue pseudonigricans". Finally, the population of "blue pseudonigricans" does not have the long snouted appearance. This is due to a dorso-ventrally less narrowed snout region and a straight, instead of an incurved dorsal head profile.

We know little about the ecology of *H.* "long snout pseudonigricans". It lives at water depths of 1.5 to at least 6 m. At the Nyegezi rocks it inhabits an almost vertically dropping slope with huge rock boulders, at Kissenda Island a moderately steep slope with boulders of medium size. It does not inhabit a gently sloping area of Kissenda Island with smaller boulders. *H.* "long snout pseudonigricans" lives sympatrically with several other species of this complex at Nyegezi rocks: *H.* "black pseudonigricans", *H.* "black and yellow pseudonigricans", *H.* "large eye pseudonigricans" and *H.* "pseudoblue". At Kissenda Island, where it coexists only with *H.* "blue pseudonigricans", it appears that "long snouts" dominate more inshore, while "blues" are restricted to more offshore waters. Judging from their numbers in our nets, the densities of the two species are offshore approximately equal.

Anatomically similar to the aforementioned species is ***Haplochromis*** **"pseudo blue"**. However, it has a different dentition that is quite unusual for this species complex. Moreover, also its male coloration is unique within the "Pseudonigricans" species. We know "pseudoblue" only from a part of the Mwanza Gulf between Python Islands in the south and Hippo Island in the north. It is abundant only in the deeper waters of the Python Islands, while very rare at Kilimo Island, Nyegezi rocks and Hippo Island. Males at Python Islands are dichromatic (Seehausen & Bouton 1996b). The coloration of the blue morph ranges from iridescent metallic blue flanks with a purple hue and a darker dorsum, to metallic purple-blue. The blue is never as clear a sky blue as in *H.* "blue pseudonigricans". All unpaired fins are purplish blue, the dorsal fin carries a lighter silvery purple, metallic iridescent band in its spiny part. Instead of the bright red streaks that characterize *H.* "blue pseudonigricans", *H.* "pseudoblue" exhibits dull red-brown streaks on the membranes of the soft dorsal. Males of the red morph have the dorsal head surface, dorsum, chest, and upper half of the flanks purplish red to red. The dorsal fin is red, and the metallic iridescence on the flanks is more yellowish than blue. Large adult males demonstrate up to eight big orange-yellow to white-yellow egg dummies. In smaller males the egg dummies are much smaller in relation to the fin. Females are greyish with a distinct silvery metallic sheen on the flanks. Males from Kissenda Island and Nyegezi rocks resemble the blue morph from Python Islands but have a reddish dorsum, more and brighter red in the unpaired fins and smaller orange coloured egg dummies. The only male from Hippo Island had lost its colours in the net. The coloration of the northern most population is therefore not yet known.

When we first collected *H.* "pseudoblue" in 1991, at a time when very few rock-dwelling cichlids were known yet, N. Bouton and I were struck by the resemblance between this species and the sympatric *H.* "blue pseudonigricans", and therefore named it *H.* "pseudoblue". However, "pseudoblue" differs distinctly from *H.* "blue pseudonigricans" and *H.* "red pseudonigricans", both of which it coexists with at the Python Islands. It has longer lower jaws and a different tooth shape. The teeth in the outer rows resemble those of the other two "Pseudonigricans" species only in small individuals, while full adults have widely, but regularly spaced, strongly recurved unicuspid teeth, resembling those of *H.* "deepwater". Large males can develop a peculiar lower jaw shape with a mental prominence ("chin").

Not much is known about the ecology of *H.* "pseudoblue". The very low water transparency at Python Islands prevents observations in its natural habitat. It lives at Python Islands at water depths ranging from 2 to 8 m, but predominantly deeper than 4 m. It tends to occur slightly deeper than *H.* "blue pseudonigricans". At the other localities we caught it at similar depths (4-7 m). Its clustered occurrence in our nets at Python Islands suggests that *H.* "pseudoblue" forages in shoals of fishes of one size class. Our stomach content analyses suggest that we are dealing with a real zooplanktivore. The three individuals checked had their stomachs to 50%, 93% and 95% filled with zooplankton (*Daphnia*). The rest were a few insect larvae, but one fish had eaten a larger amount of filamentous green algae (*Cladophora*) that it must have ingested in shallow water! The size class distribution in our catches from different seasons of the year suggests that *H.* "pseudoblue" might be a seasonal spawner. In January and February we caught almost exclusively semi-adults of between 8 and 10 cm SL, as well as some very big adults. Until April the size of the semi-adults increased, and between September and November only full grown adults were caught. The maximum size attained is 110.2 mm SL. Like in many other *Mbipi*, females are much less frequently caught than males.

The rarity of this species at any place, except Python Islands, may be a consequence of the Nile perch upsurge. Piscivorous stages of the Nile perch are abundant in the deeper waters at rocky shores in the Mwanza Gulf. Several rock-dwelling haplochromine species of deeper waters, that are elsewhere rare or entirely absent, survived in a rocky trough between the Python Islands that may offer more protection against Nile perch predation than open slopes of rocky islands do (Seehausen et al. in press [b]).

In our extensive sampling of the Mwanza Gulf we came about several individuals of "Pseudonigricans"-like fishes that do not fit into any of the known species. It may well be that at least one more

A male *H.* "black Ukerewe" (Gana).

A female *H.* "black Ukerewe" (Bihiru).

H. "longsnout pseudonigricans" (Kissenda).

A female *H.* "longsnout pseudonigricans".

A male *H.* "pseudoblue" (Python Island).

A female *H.* "pseudoblue" (Python Island).

species of this complex occurs in the region. N. Bouton and me collected in 1991 several large males at Python Islands which we named ***Haplochromis* "yellow blue"**. On the same day large males of *H.* "blue pseudonigricans" and *H.* "pseudoblue" were collected, from which *H.* "yellow blue" was clearly distinct in head shape and coloration. These fishes had a more decurved dorsal head profile, were brassy-yellow rather than blue, and had red fins similar to those of *H.* "blue pseudonigricans". They were caught at depths beyond 4 m. In spite of intensive sampling at Python Islands, fishes of this phenotype were not caught again afterwards.

A small islet of the Vesi Archipelago.

Chessboard *Mbipi*

The rock-dwelling haplochromine species joined in this group share a melanin pattern in which the dark vertical bars are crossed by two dark longitudinal stripes (mid lateral and dorsal lateral stripe), reminding of a chessboard. The so by melanin pattern defined group corresponds to Greenwood's *Paralabidochromis* lineage that was defined on anatomical criteria. All known rock-dwelling species with a chessboard melanin pattern possess a dentition that is similar to the one described for *Paralabidochromis* (Greenwood 1980). This is: rather narrow dental arcades and the anterior teeth in the lower jaw procumbently implanted, forming with those in the upper jaw a forceps-like construction (compare text figure 5). In most species the teeth of the outer tooth row are more or less cylindrical in cross section, the crowns not flattened (some species in the "Rockkribensis" complex make an exception to this). Most species have slightly thickened lips, two have their lips produced into lobes. The procumbent implantation of the outer teeth anteriorly in the lower jaw is due to a slight to moderate ventral inflection of the dentary (tooth carrying lower jaw bone), which the species of this group share with the species of the *Psammochromis* and *Ptyochromis* lineages, and with the non-rock-dwelling monotypic genera *Macropleurodus, Platytaeniodus* and *Hoplotilapia*. In most species of the Chessboard *Mbipi* the teeth in the outer rows are firmly, not moveably implanted. All but one lineage of Chessboard *Mbipi* have small, rather deeply embedded chest scales, though the expression of this character is in the "Rockpicker" group more distinct than in others. In several characters the chessboard group exceeds the limits set by the definition of Greenwood's *Paralabidochromis*. So do several species exhibit a retrognathous lower jaw, rather than isognathous jaws, and in the same species the lower jaw is not always longer than broad. Nevertheless, I think that with moderate revision of its definition, the taxon *Paralabidochromis* would be suitable to carry all rock-dwelling cichlids with a chessboard melanin pattern. However, since *Paralabidochromis* was already by Greenwood defined much wider than, for instance, *Neochromis* and *Xystichromis*, it may, alternatively, be split up into its distinct lineages.

Within the Chessboard *Mbipi*, two major groups can be identified, and within each of them again two species complexes, falling apart on gross morphology. The first group is characterized by a long head (> 33% of SL). It contains the *H. (Paralabidochromis) chilotes* complex and the *H. (P.) chromogynos* complex. The second group, with a shorter head, falls apart into a relatively long jawed (lower jaw > 34% HL) group: the *H. (P.)* "rockkribensis" complex, and a short jawed group: the *H. (P.)* "rockpicker" complex. At least one of the currently described *Paralabidochromis* species corresponds to each of these groups. Within *Paralabidochromis* a fifth group, the *H. (P.) crassilabris* group, exists but has not been found in rocky habitats.

The short head Chessboard *Mbipi*: **Tiny mouths — the *Haplochromis (Paralabidochromis)* "rockpicker" complex**

Within the chessboard species the species of the "Rockpicker" complex are readily recognized by the combination of a short head (head length of less than 33% of the standard length) with a short lower jaw (lower jaw length not exceeding 35% of the head length). It is a rather close-knit complex of species that share the following unique character combination: a peculiar small mouth; narrow, V- or U-shaped dental arcades; strong unicuspid or bicuspid and somewhat recurved outer teeth; 2 to 5 rows of inner teeth; moderately steep and slightly concave or straight, to steep and decurved dorsal head profile; a lower jaw length of 28.5-34.3% of head length; a lower jaw length/width ratio ranging from 1.07 to 1.31; an interorbital width of between 19.6 and 25.4% of head length; small deeply embedded chest scales, and between 5 and 7 vertical bars on the flanks. I assume that the species of the "Rockpicker" group form a monophyletic assemblage within the *Paralabidochromis* lineage.

All known species of this complex are morphologically specialized epilithic *Aufwuchs* feeders. In contrast to the other large anatomically specialized epilithic *Aufwuchs* feeder complex, the *Neochromis* lineage, the "Rockpicker" species forage predominantly on animalous components of the *Aufwuchs*, and on small insect larvae (Chironomidae) in particular. These tiny insects live among the filamentous algae that cover the rocks, and can sometimes at places occur in great densities. Different from many other *Mbipi*, "Rockpicker" species hardly ever took our worm-baited hooks. This may reflect their specialized feeding habits. At most places the species of this complex occur in low population densities. However, there are remarkable exceptions that show that "Rockpickers" can numerically dominate the rock cichlid community. Like in all other species complexes of *Mbipi*, one species has a wide geographical distribution (matrix species). Many others have narrow geographical ranges, and several have strongly declined recently, or went even extinct. Circumstantial evidence suggests that increasing water pollution could be a cause.

Among the described species of the *Paralabidochromis* lineage, *H. (P.) paucidens* Regan 1921, an endemic of Lake Kivu, shares all above mentioned anatomical characters with the Lake Victoria "Rockpickers" and, based on these, should be considered a member of the "Rockpicker" complex. However, it does not seem to have a chessboard melanin pattern. Snoeks (1994) when discussing the ecology of *H. (P.) paucidens*, made the observation that, though evidently insectivorous, the species does not correspond anatomically to the insect eating haplochromines of Lake Victoria, as defined by Witte & van Oijen (1990). However, as shown in the following, this apparent problem is explained by the circumstance that few rock-dwelling cichlids were known by the time Witte & van Oijen published their key to the trophic groups. Those few were meant by the authors, when they mentioned that a number of insect eating species have more specialized features.

Another species that corresponds closely to some "Rockpickers" is the mysterious *H. (P.) victoriae* Greenwood 1956. It is, among others, this species that fuelled discussion about the phylogenetic relationship between Lake Victoria and Lake Malawi (Nyasa) haplochromines (Greenwood 1956b, Greenwood 1983), since it closely resembles the Malawi genus *Labidochromis* in some anatomical characters. Unfortunately described from a single individual, it is the type species of Greenwood's genus *Paralabidochromis*. Different from all known "Rockpickers", *H. (P.) victoriae* possesses large scales on the chest. Judging from the morphometric data available from the description of *H. (P.) victoriae,* it is otherwise closest to *H. (P.)* "pseudorockpicker".

The intra-complex taxonomy of "Rockpickers" is complicated by the circumstance that most populations differ in coloration and/or other morphological characters from most other populations. This indicates pronounced site fidelity among these highly stenotopic species. Based on morphology (excluding coloration) three groups can be identified. One has (within the above defined range) a relatively long, lower jaw that is isognathous with the upper jaw (compare text figure 7f), and typical picker dentition that is similar to that of the Lake Malawi genus *Labidochromis* (outer teeth usually tend-

A reddish male *H*. "pseudorockpicker" from Kilimo Island.

A male *H*. "pseudorockpicker" from Kilimo Island.

ing to unicuspid, inner tooth rows fewer than in the other groups). A second one has a very short, retrognathous, V-shaped lower jaw that is as broad as it is long, a peculiar dentition with a rather V-shaped dental arcade, strong unequally bicuspid to unicuspid outer teeth that are inclined towards the median, and a relatively broad interorbital width. The third group has a moderately to very short, U-shaped lower jaw, that is isognathous with the upper jaw, or slightly retrognathous. It has a rather U-shaped dental arcade and scraper dentition (bicuspid outer teeth, many inner rows). In the distribution of "Rockpicker" species two patterns can be discerned: (1) The Mwanza Gulf and Speke Gulf/open lake region have different sets of species. (2) In most, if not all cases of occurrence of more than one "Rockpicker" complex species at a locality, the sympatric species belong to two different morphological groups, one being morphologically more a picker, the other one more a scraper. In the following I discuss the species in the order of the three morphological groups. The first four species belong to the long jawed picker-type group.

Rockpickers with relatively long jaws

***Haplochromis (Paralabidochromis)* "pseudorockpicker"** was first identified by Els Witte-Maas and Frans Witte who collected it at Mushroom Island/Nyegezi rocks in the northern Mwanza Gulf as early as 1978 (Witte et al. 1992). The name "pseudorockpicker" goes back to that time. Witte-Maas and Witte had collected, and named *H. (P.)* "rockpicker", what they first thought was only one species. Later they realized that their samples consisted of two different species and they called the second one "pseudorockpicker". It has a longer and narrower lower jaw than "rockpicker". Jaw and dental arcade are V-shaped rather than more U-shaped, the outer teeth tend towards unicuspid and male coloration is different from that of "rockpicker". From "southern pseudorockpicker" it differs in male coloration and outer tooth shape, from "red pseudorockpicker" in male coloration and the number of inner tooth rows (table 3), from "chessboard picker" in male coloration and eye size. All remaining species of the "Rockpicker" complex have shorter and broader lower jaws, and bicuspid outer

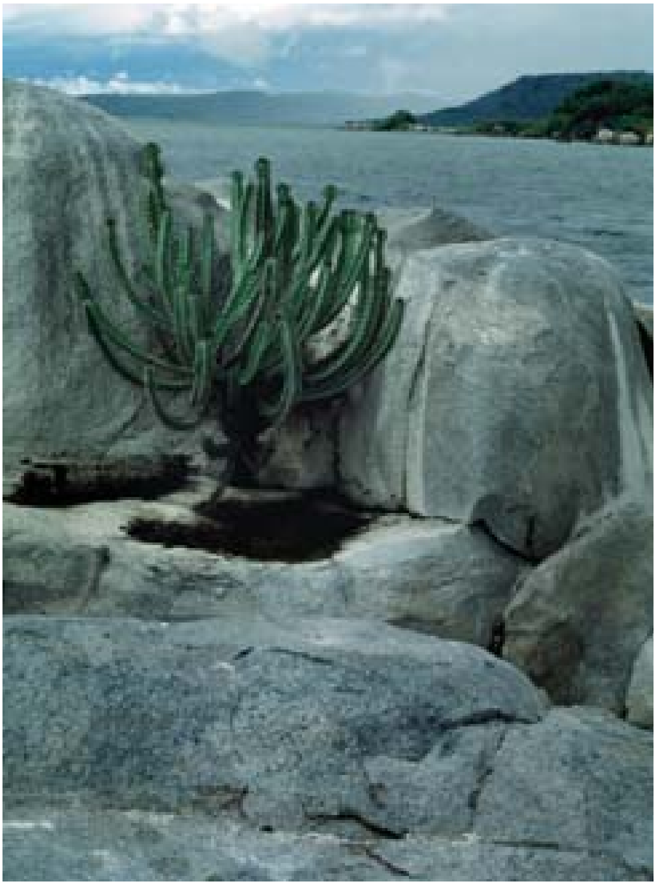
A male *H.* "southern rockpicker" (Sh).

A male *H.* "red pseudorockpicker" (Anchor Is.).

teeth. Males in breeding coloration have light blue to light greenish flanks, rarely a reddish flush on the dorsal head surface and chest, a light blue dorsal fin with red streaks in the soft part and red lappets, an entirely red caudal fin, and a yellow to light red anal fin (whitish in preserved specimens). The pelvic fins are usually black. Five to seven vertical bars are on the flanks.

The population of Mushroom Island seems meanwhile extinct, but we found "pseudorockpicker" at three other places. At Python Islands we found, in spite of extensive sampling, only one individual. Another one has been caught in 1990 by Niels Bouton, but the species must be extremely rare at that place. Higher population densities exist at Kilimo and Hippo Islands. At Kilimo Island, *H. (P.)* "pseudorockpicker" can be found at water depths ranging from 1.5 to at least 4 m. At Hippo Island it seems to be confined to slightly deeper waters, between 4 and 8 m depth. At both places the slope is moderately steep and the boulders are of medium size. Of two males that we checked from Kilimo Island, one had eaten almost exclusively chironomid larvae, the other one filamentous blue-green algae and chironomid larvae.

The populations of Kilimo and Hippo Islands differ in their morphology, particularly in lower jaw length, and outer tooth



A south-west view from Python Island.

shape, probably reflecting limited gene flow between them. The species is not known from outside the Mwanza Gulf. *H. (P.)* "pseudorockpicker" used to live in sympatry with *H. (P.)* "rockpicker" and *H. (P.)* "elongate rockpicker" in the past, and its Hippo Island population lives geographically very near to a record locality of *H. (P.)* "yellow rockpicker" (Kissenda Island), making at least parapatric contact between the two species likely. A superficially similar species that lives sympatrically with "pseudorockpicker" is *H. (P.) plagiodon.* It is not a real rock-dweller but can sometimes be seen in rocky habitats. It differs from *H. (P.)* "pseudorockpicker" anatomically (table 3 versus table 4) and in coloration. Male *H. (P.) plagiodon* have a red soft part of the pelvic fins.

Known only from the central and southern Mwanza Gulf south of Python Islands is a dull coloured species, ***Haplochromis (Paralabidochromis)* "southern pseudorockpicker"**. It differs from "pseudorockpicker" in coloration and by having bicuspid, scraper-like teeth in the outer tooth rows, although it has only two rows of inner tooth. Both sexes are brassy yellowish with the metallic sheen and light underparts that is typical for many rock cichlids in the murky waters of the southern Mwanza Gulf. We found it at a steeply sloping rock wall at about 6 m depth, as well as along a very gently sloping slab shore with sand/slab mixed bottoms at 1.5 to 2.5 m depth. It was everywhere rare.

Similarly rare and therefore poorly known is ***Haplochromis (Paralabidochromis)* "red pseudorockpicker"** which we found only at Anchor Island in the northern Mwanza Gulf. Its mouth shape is very similar to that of "pseudorockpicker" but it has a more elongate body shape, a narrower head, and males are reddish with a red soft part of the pelvic fins. Furthermore "red pseudorockpicker" has more inner tooth rows. The number of vertical bars on the flanks is about six. From *H. (P.) plagiodon*, which also occurs at Anchor Island, and has the same pelvic fin coloration, it differs by means of the narrow head as well as by a shorter lower jaw (compare tables 3 and 4). From the similarly coloured *H. (P.) crassilabris*, which lives in macrophyte rich sand bottom habitats in the Mwanza Gulf, "red pseudorockpicker" differs by its narrower head and much narrower lower jaw and dental arcades. The teeth in the outer row are a mixture of unicuspids and bicuspids that are widely spaced and recurved. We know "red pseudorockpicker" only from two individuals that we found at Anchor Island in inshore shallow water. The habitat consists of big, steeply sloping boulders. *H. (P.)* "rockpicker" used to be found at Anchor Island as well in the past. I cannot exclude that "red rockpicker", like other "rockpicker"-species of the Mwanza Gulf, was more abundant and/or more widely distributed before the large scale ecological changes in Lake Victoria began.

***Haplochromis (Paralabidochromis)* "chessboard picker"** was discovered just in 1996. Extreme rarity or geographically very restricted distribution are responsible for this. We discovered "chessboard picker" in waters of about 6 m depth at one of the small islets in the Vesi Archipelago (central Speke Gulf). The islet consists of big to huge rocks that slope steeply. In this habitat, it is the only "Rockpicker" at Vesi Islands, while *H. (P.)* "yellow rockpicker" is very abundant at less steep shores with smaller boulders. While in coloration this species reminds of *H. (P.)* "rockkribensis", it is anatomically a member of the picker-type group in the "rockpicker" complex, with unicuspid outer teeth. The only known male is yellowish with an orange flush on the chest and two prominent longitudinal stripes. The dorsal fin has red lappets and red streaks in its soft part, the proximally yellowish-grey caudal fin is distally red and the proximally grey anal fin is distally orange-red with small orange-yellow egg dummies. *H. (P.)* "yellow rockpicker" of Vesi Islands is much more greenish, has a different body shape, less prominent horizontal but more prominent vertical bars, and very different dentition. Phylogenetic affinities of "chessboard picker" are quite unclear.

Rockpickers with a short V-shaped lower jaw

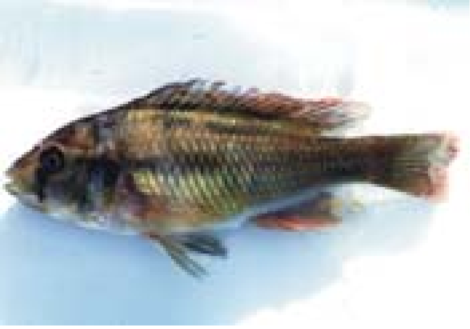
Haplochromis (Paralabidochromis) **"yellow rockpicker"** is a representative of the second morphological group of "Rockpickers". It is the geographically most widely distributed among the currently known "Rockpicker" species, and the matrix species of the complex. It has one of the shortest lower jaws that occur in "Rockpickers" and in Lake Victoria haplochromines in general. At many localities "yellow rockpicker" is characterized by yellow male body coloration, accompanied by red coloration in the unpaired fins: streaks in the dorsal fin, an entirely red caudal fin and an orange coloured to red anal fin. The pelvic fins are black. Females are light yellowish to brownish. Both sexes carry 6 to 8 vertical bars and sometimes weak traces of two longitudinal bands on the flanks. Males from Chamagati Island can exhibit an orange coloured chest. The intensity of the yellow flank coloration varies among populations. It is noteworthy that males are particularly bright yellow in populations that live in sympatry with other (always blue) "Rockpicker" species ("blue rockpicker" at Chamagati and Makobe Islands, "orange anal picker" at Bwiru Island). In contrast, males in some populations at isolated offshore islands, that are inhabited by only one "Rockpicker" (e.g. Ruti, Mabibi, Vesi Islands), are much less yellow, and often more greenish (see photos). So do the flanks of the population from Vesi Islands carry various hues from yellow-green to deep blue, contrasting beautifully with an orange to red anal fin. Apart from male coloration, also number of vertical bars, lower jaw shape, and dentition help to tell "yellow rockpicker" apart from "blue rockpicker". The outer teeth of "yellow rockpicker" are stronger, the rows of inner teeth fewer, separated from the outer ones by a broader gap (see table 3). Lower jaw and dental arcade are slightly more V-shaped in *H. (P.)* "yellow rockpicker". Its dorsal head profile is less rounded but more straight, sometimes with a small concavity above the eyes. It has 6-8 vertical bars on the flanks (versus 5-6 in "blue rockpicker"), and less prominent longitudinal stripes.

H. (P.) "yellow rockpicker" is known from almost all sampled places in the Speke Gulf and from many places in the Sengerema region. In the Mwanza Gulf, in contrast, we found it only at one place near the entrance of the Gulf (Kissenda Island) and it is very rare there. At Zue Island in the north-central Speke Gulf it is replaced by a similar but taxonomically difficult population (see below).

The habitats of "yellow rockpicker" are quite diverse and include very gentle to moderately steep slopes. The species is absent from habitats with very steep slopes (several islets within the Vesi Archipelago) or is very rare in such habitats (Ruti Island). It is very impressive in this respect, to observe the enormous abundance of "yellow rockpicker" at moderately steep slopes in the Vesi Archipelago (numerically a co-dominant species, together with *H. (Neochromis)* "Vesi scraper"), and its complete absence from steep slopes just a few hundred metres further. At the moderately steep slopes it lives at water depths ranging from 1.5 to at least 5 m and is most abundant at about 3 to 5 m. At Mabibi Islands, in a similar habitat, it is common, though not dominant, at 2 to 5 m depths, and is absent from depths beyond 5 m. At other localities it inhabits a similar depth range but is much more rare, so that actual depth preferences are difficult to observe. While I frequently observed subadult and adult *H. (P.)* "blue rockpicker" when diving at Makobe Island, I only once came across a *H. (P.)* "yellow rockpicker". This was a full adult male that seemed to be having a territory at only 1.5 m water depth. At the well studied island, "yellow rockpicker" seems to undergo considerable fluctuations of population density. Of three males from Makobe Island whose stomachs we checked, two had eaten almost exclusively chironomid larvae, the third one filamentous green algae, unicellular algae and plant material, which it probably ingested as detritus (see the discussion under *Xystichromis)*.

H. "yellow rockpicker" from Makobe Island.

A male H. "yellow rockpicker" from Bwiru Island.



A male *H*. "chessboard picker" (Vesi Is.).

A male H. "yellow rockpicker" from Vesi Island.

A female H. "yellow rockpicker" (Sozihe Is.).

H. (P.) "yellow rockpicker" occurs sympatrically with *H. (P.)* "blue rockpicker" at Makobe and Chamagati Islands, with *H. (P.)* "elongate rockpicker" at Ruti Island, with *H. (P.)* "orange anal picker" at Bwiru Island and with members of all other spe-

A male *H*. "Zue rockpicker" (Zue Island).

A female *H*. "Zue rockpicker" (Zue Island).

cies complexes of the Chessboard *Mbipi*.

Anatomically very similar to *H. (P.)* "yellow rockpicker" is a "Rockpicker" population from Zue Island in the central-northern Speke Gulf, which bears the melanin pattern of *H. (P.)* "blue rockpicker" and a male coloration that also resembles that of the latter species. In contrast to all typical populations of "yellow rockpicker", this one has only 5 to 6 vertical bars on the flanks which are crossed by well visible longitudinal stripes. The anal fin is pale with slight pinkish flush and their is very little red also in the other unpaired fins. I am currently not able to say whether **"Zue rockpicker"** is an aberrantly coloured population of "yellow rockpicker", an anatomically aberrant "blue rockpicker", a result of hybridization between the two species, or something completely different. It lives between less than 1 and at least 4.5 m water depth at a very gently sloping shore with very small boulders and stones and can be rather abundant at about 3 m depth.

The north-eastern corner of Gana Island, habitat of *H*. "orange anal picker".

Rockpickers with scraper dentition

***Haplochromis (Paralabidochromis)* "rockpicker"**, discovered by F. Witte and E.L.M. Witte-Maas in the late 1970s in the Mwanza Gulf (Witte et al. 1992), was the first known representative of the third morphological group, the scraper type of "Rockpickers". Witte and Witte-Maas used to collect it by worm-baited hook at rocks in the Nyegezi area and at Anchor Island (northern Mwanza Gulf). Between the early 80s and the late 80s the species disappeared from its former localities. One male was still collected by N. Bouton and me at Mushroom Island in 1991. In spite of intensive sampling there and at many other places, no further individual was seen after that. Considering the apparently very small geographical range that this species had, it is possible that it is extinct. Male "rockpicker" in breeding dress are, according to Witte and Witte-Maas (pers. comm.), grey-black to blue-grey, with 6-7 vertical bars on the flanks. The dorsal fin is dark grey with a blue sheen, red spots in the soft part and red lappets. Caudal and anal fin are dark greyish near the basis and red distally. Females are dark grey-brown above, silver-white below, and bear a distinct chess-board melanin pattern. The dorsal head profile is decurved, the lower jaw slightly retrognathous. The lower jaw is U-, rather than V-shaped, the teeth in the outer row are bicuspid, and the number of inner tooth rows is increased (table 3). By these characters *H. (P.)* "rockpicker" differs distinctly from the sympatric *H. (P.)* "pseudorockpicker" and *H. (P.)* "red pseudorockpicker", but is close to *H. (P.)* "orange anal picker" and *H. (P.)* "elongate rockpicker". From the first it differs in male and female coloration, from the latter in dentition and body shape.

The rocky habitats that were inhabited by *H. (P.)* "rockpicker" in the central and northern Mwanza Gulf, slope moderately steeply to steeply and have medium sized to large rock boulders. The information available, suggests that the species was preying predominantly on chironomids (Witte & Witte-Maas pers. comm.), like all other "Rockpickers" do, about whose feeding habits we have information. *H. (P.)* "rockpicker" lived sympatrically with *H. (P.)* "pseudorockpicker" and *H. (P.)* "elongate rockpicker" at Nyegezi rocks, and with the latter and *H. (P.)* "red pseudorockpicker" at Anchor Island (Witte & Witte-Maas pers. comm.). Other sympatric *Paralabidochromis* were *H. (P.)* "rockmacula", *H. (P.)* "rockkribensis" and *H. (P.) plagiodon*.

Another species of the scraper type is ***Haplochromis (Paralabidochromis)* "orange anal picker"**. It has an even shorter lower jaw than "yellow rockpicker" and there is hardly any overlap between the two species with regard to this character. *H. (P.)* "orange anal picker" is known from only two localities, both in the western Ukerewe region, though quite far from each other. Since the extensive rocky shores between the two places have not been sampled, it is not known, whether the species has a closed distribution in western Ukerewe. However, the two populations differ in some morphometric measurements so considerably that I would probably consider them specifically distinct, would they not have a very similar male coloration. Males are dark grey with a beautiful metallic deep blue (Gana Island) or blue-green (Bwiru Island) sheen on the whole body, and a metallic blue or blue-green dorsal fin with red lappets. There are 7-8 (Gana Island) or 6-7 (Bwiru Island) vertical bars on the flanks. The caudal fin is bright red and the anal fin orange with small (Bwiru Island) to very small (Gana Island) egg dummies. Females are known only from Bwiru Island yet. They are very similar to those of "yellow rockpicker" but have an even shorter, more tiny lower jaw. Small but significant differences between the two populations of "orange anal picker" exist in maximum size (Gana > Bwiru), body depth (Gana < Bwiru), head length (Gana < Bwiru), and eye length (Gana < Bwiru). Moreover, fishes from Gana Island have a more rounded dorsal head profile. *H. (P.)* "orange anal picker", particularly of Gana Island, are anatomically a peculiar appearance. They have the shortest lower jaw that I have measured among Lake Victoria haplochromines (one male with a lower jaw length of 27% of the head length; Witte & Witte-Maas [pers. comm.] once had a "rockpicker" with a lower jaw length of only 25.5% of the head length). This lower jaw is often retrognathous, however, since also the upper jaw is short, the jaws are sometimes isognathous. With the elongated body and rounded dorsal head profile, the fishes strongly resemble algae scrapers of the *Neochromis* lineage, and are almost certainly confused with such before one realizes the jaw shape.

H. (P.) "orange anal picker" is also ecologically similar to *Neochromis* species, especially to *H. (N.)* "blue scraper" with which it lives in sympatry at both record localities. At Gana Island "orange anal picker" is observed at depths between 1.5 and 6 m. It is at some spots the numerically dominant haplochromine at 2 to 4 m depth, especially in the wide and deep crevices and gorges between big rock boulders. There seems to be a tendency for *H. (Neochromis)* "blue scraper" to occur in more shallow water, and I observed territorial males only at less than 2 m depth. Males of "orange anal picker" defend territories among the big rock boulders at depths between 1.5 and 3 or 4 m (beyond that depth *H.* "lemon fin nyererei" are the dominant territory holders). Vertical and horizontal gaps in rock walls frequently form the centre of a territory. From such a hiding place males approach females, and I saw them entering into the plankton grazing shoals that are dominated by female *H.* "lemon fin nyererei". Possibly female "orange anal picker" join these shoals in the water column of rocky gorges. A very similar picture of depth preferences is observed at Bwiru Island: At water depths down to 2.5 m *H. (N.)* "blue scraper" numerically dominates and *H. (P.)* "orange anal picker" is very rare. Just below 2.5 m depth the ratio of abundance turns sharply, and already at 3-4 m depth "orange anal picker" is often ten times more abundant than "blue scraper", and can be the dominant haplochromine. At yet greater depth (beyond 4.5 m) *H. (Neochromis)* "long black" takes over. *H. (P.)* "yellow rockpicker" and *H. (P.)* "red short snout scraper" that also live at Bwiru Island, have their maximum abundance at 2-3 m depth. Finally, "yellow anal picker" lives in sympatry with *H. (P.)* "sky blue picker" at Gana Island.

F. Witte and E.L.M. Witte-Maas caught in the 1970s a species of the "Rockpicker"-complex with a particularly shallow, elongated body shape. They named it ***Haplochromis (Paralabidochromis)* "elongate rockpicker"**. This species has disappeared from its former localities in the northern Mwanza Gulf (Nyegezi area, Anchor Island) just like *H. (P.)* "rockpicker" has. We have, however, recently come about a shallow bodied "Rockpicker" at Ruti Island, that may be identical with *H. (P.)* "elongate rockpicker". The male is rather dark blueish with an orange-red anal, a dark dorsal fin with broad red lappets and a caudal fin that is dark at its base and red distally. This species has one of the most extreme scraper dentitions within the "Rockpicker" complex. The outer tooth row consists of closely set subequally bicuspid teeth with slightly recurved crowns, and the inner teeth are arranged in about 5 rows (table 3). "Elongate rockpicker" is morphologically very close to "orange anal picker". It differs from the latter by means of a longer lower jaw and narrower head. However, it is not impossible that the two forms turn out to be conspecific, once more is known about the very rare "elongate rockpicker". Nothing is known about the feeding ecology of this species. It lives in sympatry with *H. (P.)* "yellow rockpicker" and is the more rare one of the two.

Another typical representative of the "Rockpicker" species with scraper dentition is ***Haplochromis (Paralabidochromis)* "blue rockpicker"**. It is characterized by light blue male body coloration, and a prominent melanin pattern. The dorsal fin is blue, sometimes with red streaks in the soft part and with red lappets. Anal and caudal fin are red. Under water the anal fin appears pale, while the caudal fin bright, resembling that in *H. (Neochromis) nigricans*. The pelvic fins are black. Females are silvery whitish, rather than yellowish to brownish as those of the sympatric *H. (P.)* "yellow rockpicker". Both sexes exhibit a distinct chessboard pattern of almost always six vertical bars and two longitudinal bands on their flanks. The prominent appearance of the latter helps to distinguish females of the blue species from those of the yellow species. The dorsal head profile of "blue rockpicker" is steep, usually decurved, rounded and never concave. The dentition of *H. (P.)* "blue rockpicker" differs from that of all aforementioned species. The outer teeth are rather fine, subequally to unequally bicuspid and very closely set. The inner teeth are very small tricuspids and arranged in up to 7 rows in the upper, and up to 4 in the lower jaw. The gap separating them from the outer teeth is less broad than in *H. (P.)* "yellow rockpicker", and can be almost absent. The dentition of *H. (P.)* "blue rockpicker" thus resembles that of the algae scrapers of the


A male *H*. "rockpicker" (Python Island).


A male *H*. "elongate rockpicker" (Ruti Island).


A male *H*. "orange anal picker" (Bwiru Is.).


A male *H*. "orange anal picker" from Gana Island.


A female *H*. "blue rockpicker" (Makobe).


A male *H*. "blue rockpicker" from Nansio.

A male *H.* "blue rockpicker" from Makobe in the aquarium.

A female *H.* "blue rockpicker" with fry.

Neochromis-lineage. Like in some of the latter (e.g. *H. (N.) nigricans*), the inner teeth can be arranged in a zigzag pattern that partly obscures the rows. However, the outer teeth in the lower jaw are procumbent, and the dental arcades have the narrow shape of the "Rockpicker"-complex, though resembling more a U than a V. The jaws are isognathous. Similar to *H. (P.)* "blue rockpicker" are *H. (P.)* "elongate rockpicker" and *H. (P.)* "rockpicker". The first one differs in body shape, dentition and coloration, the second one in dentition and coloration.

H. (P.) "blue rockpicker" has a relatively wide geographical range but a very scattered distribution. We know it from Nansio (Ukerewe) at the northern shore of the Speke Gulf, from Makobe Island in the southern Speke Gulf entrance, and from Chamagati Island in the Sengerema region. The habitat at two islands is a gentle (Makobe) to very gentle (Chamagati) slope, with small to very small rock boulders. At Nansio the slope is steeper, and the boulders are bigger. It is unclear, why the species is absent from other islands with apparently suitable habitat, e.g. Matwinki Island (near to Chamagati Island) and Igombe Island (near to Makobe Island). At Makobe Island adults inhabit slightly offshore water depths between 2 and 6 m, while we observed juveniles and subadults up to 5 cm SL frequently in very shallow inshore waters. We measured maximum population densities of adults at 2 to 4 m depth (Seehausen & Bouton in press). At Chamagati Island adult "blue rockpicker" live between 1.5 and at least 3 m water depth. At both places the species is more abundant than "yellow rockpicker". At Nansio it lives at depths between 2 and at least 4.5 m. Scuba observations at Makobe Island revealed that adults and subadults forage in small groups of two to four individuals or solitary.

Among 11 male "blue rockpicker" that we checked (7 from Chamagati Island, 4 from Makobe Island), four had empty stomachs, four had eaten predominantly chironomid larvae, one mayfly (Ephemeroptera) larvae, filamentous blue-green and green algae, one diatoms and one unidentified material. All those that had eaten insects had consumed considerable amounts of various types of algae with them. The one that had eaten predominantly diatoms had eaten also some chironomids. Thus the diet of this species is very similar to that of "yellow rockpicker", with whom it lives in sympatry (the ratio insect larvae versus algae is slightly lower in the blue species). Like most "rockpicker" complex species, also *H. (P.)* "blue rockpicker" almost never (one exception) took our worm-baited hooks. In laboratory experiments in aquaria, "blue rockpicker" foraged on epilithic *Aufwuchs* predominantly by pullscraping and picking (Seehausen et al. in press [a]). Population densities of "blue rockpicker" are moderate at all three record localities, meaning that the species is not difficult to find in its habitat but is not really abundant either. *H. (P.)* "blue rockpicker" lives sympatrically with *H. (P.)* "yellow rockpicker" and three more *Paralabidochromis* with scraper anatomy: *H. (P.)* "short snout scraper", *H. (P.)* "red short snout scraper" and *H. (P.)* "rockkribensis".

***Haplochromis (Paralabidochromis)* "sky blue picker"** is yet another light blue "rockpicker" of the scraper group. We discovered this species in early 1996 at Gana Island, at the northern limit of our survey area. It may thus be more widely distributed outside the surveyed area. This species differs from the similarly coloured "blue rockpicker" by a much longer lower jaw (the longest one that occurs in the "rockpicker" complex), a dorsal head profile that is straight to concave, and extensive red coloration in the dorsal fin in form of dots and streaks. Furthermore, the chessboard pattern is less prominent. The dentition with subequally bicuspid, closely set outer teeth and 4 inner tooth rows in both jaws is, as already in "blue rockpicker", reminiscent of *Neochromis* dentition. In the case of "sky blue picker" even the lower jaw length resembles that of many *Neochromis*, however, jaw and dental arcade are narrower than in the latter, and the teeth in the lower jaw are procumbent. The habitat of "sky blue picker" is the already mentioned rock garden of large, steeply sloping rock boulders, where we found it at 3 to 4 m water depth sympatrically with *H. (P.)* "yellow anal picker".

The *Haplochromis* (*Paralabidochromis*) "rockkribensis" complex

Among the chessboard species, the members of the "rockkribensis" complex are recognized by the combination of a short head (head length less than 33% of the standard length), with a relatively long lower jaw (more than 34% and up to 39% of the head length). Their dental arcades, though somewhat narrowed, are not as narrow as in the other species complexes of the *Paralabidochromis* lineage. Their outer teeth are usually bicuspid, with a flange on the major cusp, and the inner teeth are arranged in 2-4 rows. They have a straight to slightly concave dorsal head profile that, compared to the dorsal head profile of the "Rockpicker" complex species, slopes gently. The lower jaw is usually slightly longer than the upper jaw, and always longer than broad, with a length/width ratio between 1.16 and 1.6. The interorbital width is, with 23.7-27.7% of the head length, larger than in the "Rockpicker" complex. The chest scales are in some species larger and less deeply embedded than in most other rock restricted cichlids, or not deeply embedded at all. On the flanks are between 5 and 7 vertical bars.

Among the described species of the

Paralabidochromis lineage, *H. (P.) plagiodon* fits anatomically into the definition of the "rockkribensis" complex, and should be considered a member. However, it does not exhibit a real chessboard melanin pattern. In *H. (P.) plagiodon*, as well as in many species of the "rockkribensis" complex, a tendency to an increased number of egg dummies can be observed, and these are frequently present also in females, though usually without the transparent outer ring. *H. (P.) plagiodon* is sometimes caught in rocky habitats, but is merely an occasional intruder, coming from other habitats, rather than a permanent rock-dweller (see the chapter on frequent intruders).

Intra-complex taxonomy seems relatively simple. There are two species that are distinct from all others: *H. (P.)* "rockkribensis" and (if considered a member of the complex) *H. (P.) plagiodon*, and a complex of probably very closely related species, the *H. (P.)* "short snout scrapers". Some species of the *Haplochromis (Paralabidochromis)* "rockkribensis" complex belong to the most conspicuous Lake Victoria cichlids. Bright female coloration is a rare phenomenon among Lake Victoria cichlids, and is characteristic for certain species of this complex. Such females exhibit a deep black chessboard pattern on yellow ground colour.

Haplochromis (Paralabidochromis) **"rockkribensis"** is together with *H. (Xystichromis)* "copper black" probably the most widely and evenly distributed species among the known *Mbipi*. It is, possibly together with *H. (P.) plagiodon*, the matrix species of the "Rockkribensis" complex. *H. (P.)* "rockkribensis" was discovered by F. Witte and E.L.M. Witte-Maas in 1978 (Witte et al. 1992). We found it at most rocky places that we sampled, in big and small boulder habitats, and at steep and gentle slopes. It is known also from the northern shores of Lake Victoria (Kaufman & Ochumba 1993). Maybe the most peculiar feature of *H. (P.)* "rockkribensis" is its bright yellow female coloration, with a dark black chessboard melanin pattern. Though a trend to similar female coloration exists in at least one other species (see below), the brightness of "rockkribensis" females is unique among *Mbipi*. It is very little variable among populations and seems therefore to be evolutionary much more stable than the coloration of males. Males of most populations are characterized by a bright red chest, and an otherwise yellow body, superimposed by a faint chessboard pattern. Some populations, however, differ considerably from this coloration and, following commonly used species recognition criteria with strict application of the SMRS concept (see the chapter on taxonomy), might be regarded different species. However, because such different colour types represent exclusively allopatric populations, because differences in coloration do not seem to be correlated with anatomical or ecological differences, and because all populations share the unique female coloration, I consider them as geographical variants of one species. Among them are populations with entirely red males at islands in the northern Speke Gulf (picture) and a population with very dark, almost black males from the vertically sloping Nyegezi rocks (picture). Males from northern Lake Victoria are often rather dark (Kaufman & Ochumba 1993), and a blueish form is known (Kaufman & Seehausen 1995). Unfortunately little is known yet about the heritability of these colour traits in *H. (P.)* "rockkribensis". At least in the case of the blackish form, pigmentation might partly be a phenotypic response to the unusual light conditions in the habitat. At the vertically sloping rocks upwelling light is almost entirely lacking.

Also anatomically some variation among populations of "rockkribensis" exists, particularly with respect to the feeding apparatus. The outer tooth rows in both oral jaws are composed of bicuspid teeth. Most populations from the Mwanza Gulf and Speke Gulf have a small flange on the major cusp and three to four inner rows of teeth. However, some populations have a more epilithic algae scraper like dentition with more inner tooth rows. Other populations (e.g. that of Chamagati Island) have a more predatory appearance

A male *H.* "sky blue picker" (Gana Is.).

Kissenda Island, habitat of the normal form of *H*. "rockkribensis".

A pull-scraping *H*. rockkribensis" at Chamagati.

A female *H.* "rockkribensis" (Python Island).

H. "rockkribensis" (Python Is., normal form).

H. "rockkribensis" (Buyago, pale form).

H. "rockkribensis" (Ngoma, black form).

A male of the red form of *H*. "rockkribensis".

Matwinki Island, habitat of the red form of *H*. "rockkribensis".

A female and male *H*. "rockkribensis" (Chamagati, elongated form).

A male *H*. "rockkribensis" from the northern Mwanza Gulf.

with a slightly longer head and longer lower jaw. While populations in southern Lake Victoria possess rather fine teeth on the pharyngeal jaws, some northern (Kenyan) populations exhibit enlarged molariform teeth on these bones, typical for snail crushers (Kaufman & Ochumba 1993). The dorsal head profile of *H. (P.)* "rockkribensis" does not vary much. It is straight and rather gently sloping.

H. (P.) "rockkribensis" is largely a shallow water species, though individuals are sometimes caught at depths beyond five metres. In the well studied community at Makobe Island, it has its highest densities between 2.5 and 4.5 m depth. The only three territorial males that I saw there in many diving hours, had their territories at 1.2, 1.5 and 6 m depth. At most places, *H. (P.)* "rockkribensis" is found very regularly, but not in high abundance. However, at a few islands it is abundant, and among the dominant members of the community. Such places have a gentle slope and small to medium sized rock boulders. *H. (P.)* "rockkribensis" feeds in the southern range of its distribution predominantly on animalous *Aufwuchs*, including associated insect larvae, which it collects from the rock surface. Of three males from Makobe Island whose stomachs we checked, one had eaten predominantly filamentous blue-green algae and other epilithic algae, the second one caddis fly larvae and sponges, and the third one almost exclusively chironomids. In laboratory experiments *H. (P.)* "rockkribensis", foraging on *Aufwuchs*-covered rocks, showed a preference for moss animals (Bryozoa), which it scraped off from the rocks. In its natural habitat, the species is usually seen moving along the surface of the rocks, and does not regularly inhabit the interstices between rocks, which are home to other epilithic invertebrate eating *Mbipi*. *H. (P.)* "rockkribensis" lives at different localities sympatrically with all other species of this complex, and with most other species of chessboard-*Mbipi*.

A recently discovered group are the "short snout scrapers". The group is quite widely distributed but its representatives are almost everywhere very rare, and were therefore overlooked for long. Anatomically they are similar to "rockkribensis" but have a shorter lower jaw and bigger eyes. Male coloration of some species is very similar to that of the red populations of "rockkribensis". Females are usually yellowish brown but those of one species are yellow with a dark chessboard pattern, though not as deep yellow as "rockkribensis" females.

The mouth of "Short snout scrapers" is smaller than that of *H. (P.)* "rockkribensis", but is not as small as that of "Rockpickers". Lower jaw and dental arcade are not as narrow as in the "Rockpickers". The outer teeth are scraper teeth, mostly unequally bicuspid with flange, similar to those of *H. (P.)* "rockkribensis", sometimes subequally bicuspid and frequently, though not always, closely spaced. The number of inner rows ranges from two to five. This dentition can be somewhat reminiscent of the condition in *Neochromis*. However, the "Short snout scrapers" share with "rockkribensis" a characteristic snout shape with a slightly prognathous lower jaw, in contrast to the isognathous jaws or retrognathous lower jaw of "Rockpicker" complex and *Neochromis* species. The dorsal head profile is less steep than in most *Neochromis* and "Rockpickers". In spite of the morphological part-resemblance of some species with the *Neochromis*-complex, the "Short snout scrapers" are, with their lower jaw anatomy and melanin pattern well embedded in the *Paralabidochromis* lineage. This is the only group of *Mbipi* in southern Lake Victoria that has predominantly rather large and not deeply embedded chest scales (but see page 90 for the northern lake).

We discovered most "Short snout scraper" populations within the last two years: So also a population at Makobe Island that had already by then the best sampled rock-cichlid community in Lake Victoria. This just illustrates the low densities in most "short snout scraper" populations. With one exception, forms of the "Short snout scraper" group are allopatric. This makes it in some cases difficult to decide, whether to consider different forms as different species or as populations of one. I currently distinguish between five anatomically and in male and female coloration different species, at least two of which live sympatrically.

I consider several geographically well isolated, but anatomically and in coloration similar populations from offshore Speke Gulf islands, as a single species, to which I refer as ***Haplochromis (Paralabidochromis)* "short snout scraper"**. Such populations are known from Sozihe, Vesi, Mabibi, Ruti and Makobe Islands. In spite of much sampling we could not find any at the very gently sloping Zue Island. From the two eastern most record localities, Sozihe and Vesi Islands, male coloration is not yet known because we found only females. Males at Mabibi and Makobe Islands have grey-brown flanks with a reddish flush, a similarly coloured dorsal fin with red lappets and streaks in the soft part, a reddish caudal, and a red anal fin, with up to ten medium sized yellow-orange egg dummies. Females are dark brown with yellow flush, particularly on the fins and a faint chessboard melanin pattern on the flanks. Males of these populations usually have a peculiar rounded body shape (see photo) due to an unusually strongly convex lower body outline and a slightly decurved dorsal head profile. Females can have the same shape but can also be more elongate with a much shallower dorsal head profile. Both sexes bear six to eight vertical bars on the flanks.

Fishes from Ruti Island differ somewhat from those of Makobe and Mabibi Islands. Males have a greenish flush on the flanks and frequently an orange coloured chest, somewhat resembling *H. (P.)* "rockkribensis" that is absent from Ruti Island. Fishes from Ruti Island are smaller, their head is narrower, the ventral body outline usually less convex, and some males have a less steep dorsal head profile, which contributes to the impression that "short snout scraper" from Ruti Island slightly resembles *H. (P.)* "rockkribensis". Nevertheless, morphometrically it is close to the populations from Makobe and Mabibi Islands. At the gently sloping Makobe Island *H. (P.)* "short snout scraper" lives in the more offshore waters between 1.5 m and 6 m depth. The majority of the fishes has been found in depths beyond 3.5 m. At Mabibi Island we found a big sexually active male at about 8 m depth, at a vertically sloping rock wall. The fishes at Ruti Island live closer inshore and are most frequently found in rockpools. They, however, go down to at least 4 m depth as well.

H. (P.) "short snout scraper" may be a diatom eater. Of three males whose stomachs we checked, two had eaten almost exclusively diatoms, the third one had eaten diatoms, filamentous blue-green algae and chironomid larvae to about equal parts. Unfortunately its feeding behaviour has never been observed. The species is so rare that I have never seen it under water, and neither this one, nor any other member of the group, has ever been kept in aquaria. At Ruti Island, where "short snout scrapers" live in reach of angling lines, they readily take worm-baited hooks, in contrast to species of the "Rockpicker" complex. *H. (P.)* "short snout scraper" lives syntopically with *H. (P.)* "rockkribensis", *H. (P.)* "yellow rockpicker", and *H. (P.)* "blue rockpicker", as well as with many scrapers of the *Neochromis* lineage.

***Haplochromis (Paralabidochromis)* "red short snout scraper"** is a large growing, brightly coloured species, known from Bwiru and Ukerewe islands in the northern Speke Gulf. Among the known "Short snout scrapers" this one is anatomically, and in male coloration closest to *H. (P.)* "rockkribensis". It has a deeper body, a broader head, a larger lower jaw length/width ratio, and often a longer lower jaw than *H. (P.)* "short snout scraper" from the central Speke Gulf islands. Its outer teeth are often only weakly bicuspid. Moreover, its dorsal head profile is less steep, slightly concave and thus similar to that of "rockkribensis". Males are blue-grey to purplish grey, superimposed by a faint

The shore waters of this part of Hippo Island is home to *H*. "blue short snout scraper".

A male *H*. "red short snout scraper" from Bwiru Island.

A female *H*. "red short snout scraper" (Bwiru).

A male *H*. "red short snout scraper" (Bwiru).

A female *H*. "blue short snout scraper".

A male *H*. "blue short snout scraper" (Hippo Is.).

A female *H*. "short snout scraper" (Makobe).

A male *H*. "short snout scraper" (Makobe Island).

A female *H*. "elongate short snout scraper".

A male *H*. "elongate short snout scraper" (Hippo).

chessboard melanin pattern and bright orange to red gill cover and chest. In many adult and sexually active individuals the orange to red coloration extends across the entire lower two thirds of the flanks. Such fishes are often extremely bright and closely resemble males of the red populations of *H. (P.)* "rockkribensis". Less intensively coloured individuals can be quite similar to the "normal" (red chest) type of the latter species. Females resemble in coloration those of *H. (P.)* "short snout scraper" from the central Speke Gulf islands, rather than those of *H. (P.)* "rockkribensis". They are much less deep bodied than males.

H. (P.) "red short snout scraper" lives between 2 and at least 5.5 m water depth, syntopically with *H. (P.)* "rockkribensis". We found its highest population densities (sexually active males) in relatively surf protected situations at 2-4 m depth. It lives sympatrically, furthermore, with *H. (P.)* "yellow rockpicker", *H. (P.)* "blue rockpicker", *H. (P.)* "orange anal picker" and with several *Neochromis* scrapers.

***Haplochromis (Paralabidochromis)* "blue short snout scraper"** is another large growing and deep bodied species. It is known from Hippo Island in the entrance to the Mwanza Gulf and from Matwinki Island in the Sengerema region. A similar population from the nearby Kissenda Island may belong to this species as well. *H. (P.)* "blue short snout scraper" is distinctly different from all other members of the "Rockkribensis" complex in its male coloration. Males are light blue at Matwinki, dark blue with metallic sheen on the flanks at Hippo Island, and can there on first glance be taken for males of the sympatric *H. (Neochromis)* "velvet black". Different from the latter, they exhibit an orange-red anal fin, an orange-red to red caudal fin, similarly coloured dorsal fin lappets and streaks in the soft dorsal. Females are yellowish-brown with greenish flush, and both sexes bear five to seven dark vertical bars and two sometimes prominent longitudinal stripes on the flanks. "Blue short snout scraper" grows larger than other species of the group. At Matwinki Island we found males of above 120 mm standard length.

In its dentition this species differs slightly from other "Short snout scrapers" as well. It has frequently one more inner tooth row. While anatomically otherwise similar to "red short snout scraper" with its broad head and deep body, it differs from the latter by retaining longer its bicuspid dentition. Even males above 100 mm standard length have real bicuspid outer teeth. These morphological differences correspond to differences in the ecology. At the, on average moderately steep slope of Hippo Island these fishes show a preference for the most gently sloping places. Females and subadult males can be observed grazing *Aufwuchs* on immediately inshore, sun exposed, flat rock surfaces in the company of *H. (Neochromis) nigricans* and *H. (N.)* "velvet black". Females go down to depths of about 3.5 m, large males live at depths between 4 and maximum 7 m. Like the sympatric *Neochromis*, and in contrast to the sympatric *H. (P.)* "pseudorockpickers", this species readily takes worm-baited hooks.

Hippo Island is the only place where we found two species of the "Short snout scraper" lineage, living in sympatry. The second species, "elongate short snout scraper" resembles in its reddish male coloration the other species of the lineage. The evolution of the blue male coloration of *H. (P.)* "blue short snout scraper" may have been driven by this sympatric situation, or, the other way around, may have evolved in allopatry and consequently allowed the coexistence of two closely related species that differ in male coloration. "Blue short snout scraper" furthermore lives sympatrically with *H. (P.)* "rockkribensis", *H. (P.)* "pseudorockpicker", and *H. (P.)* "yellow rockpicker", and with the algae scrapers *H. (Neochromis) nigricans*, *H. (N.)* "black nigricans", *H. (N.)* "velvet black" and *H. (Xystichromis)* "copper black".

***Haplochromis (Paralabidochromis)* "elongate short snout scraper"**, the second species from Hippo Island, has yellowish males with a coppery to reddish coloured head, and anterior half of the flanks. Females are yellowish brown with a faint chessboard melanin pattern. Both sexes have about six vertical bars on the flanks. From other species of the "short snout scraper" lineage with reddish males, this form differs distinctly in body shape. It is much shallower than the others, has the least steep dorsal head profile, and narrower jaws, resulting in a higher length/width ratio of the lower jaw. From the sympatric "blue short snout scraper", it differs also by having usually fewer tooth rows and by greyish, rather than reddish fins, including the anal fin. It is very rare at Hippo Island, and we found it only in greater depths, between 6 and 7 m.

***Haplochromis (Paralabidochromis)* "rock macula"** resembles on the first glance *H. (P.)* "elongate short snout scraper", but differs from it in several characters. It has a greater body depth, shorter, and relatively broader jaws, and different female coloration. Its females are yellowish, with a dark chessboard pattern on the flanks, reminding of "rockkribensis" females, though the coloration is less bright. This female coloration sets the species apart from the other "short snout scrapers" with reddish males. Moreover, it differs from "red short snout scraper" by shorter lower jaws, tooth shape (almost subequally bicuspid outer teeth), and by a narrower head, and from "short snout scraper" by a much less steep dorsal head profile, and a much less convex ventral body outline. Sexually active males are brightly coloured: Gill covers, chest, belly and anterior flanks are deep blood red, the remaining body yellow. A faint chessboard pattern can be present. The dorsal fin is grey with red spots and streaks, the caudal fin is grey with some red distally, and the anal fin is pale reddish. Females can have rather large, and colourful egg dummies on their yellow anal fin.

H. (P.) "rock macula" has its name because of its superficial resemblance with the epiphythic algae scraper *H. (Haplochromis)* "macula" (page 253). It is known only from a small patch of huge rocks at the southern entrance to the Nyegezi Bay (Mushroom Island, Nyegezi rocks). There it was probably already collected in 1978 by E.L.M. Witte-Maas and F. Witte (pers. comm.) who took it for *H. (H.)* "macula", but already noted some peculiarities of the rock-dwelling "form". We observed and collected several more individuals in 1991. In 1993 we found just one male, in spite of much search. Since then the species was not seen any more. Considering its narrowly restricted distribution and the disappearance of several other rock-dwelling haplochromines from the northern Mwanza Gulf (e.g. *H. (Neochromis)* "kruising", *H. (P.)* "rockpicker", *H. (P.)* "elongate rockpicker"), *H. (P.)* "rock macula" is to be considered critically endangered, if it is not yet extinct.

Little is known about the ecology of this species. Its former habitat is composed of huge, and mostly steeply sloping rock boulders. In this environment it was found at places where the huge rocks slope less steeply, which is an uncommon habitat situation. All males that we found in 1991, were collected from crevices among rocks. *H. (P.)* "rock macula" lived sympatrically with *H. (P.)* "rockkribensis", *H. (P.)* "rockpicker", *H. (P.)* "pseudorockpicker", *H. (P.)* "elongate rockpicker" and some *Neochromis* algae scrapers. *H. (P.) plagiodon* is abundant on sandy bottoms adjacent to the huge rocks.

The study of unidentified fishes that were collected by F. Witte and E.L.M. Witte-Maas in the late 1970s in the Nyegezi, area revealed one female individual of a species of the "Short snout scraper" lineage that does not seem to be "rock macula". Thus more species of this complex may have existed in the central Mwanza Gulf by that time.

The long-head Chessboard *Mbipi*: **Lobe-lipped cichlids — the *Haplochromis (Paralabidochromis) chilotes* complex**

This is a small complex (two species), that is probably closely related to the *H. (P.) chromogynos* complex. Among the chessboard species its members are rec-

A male *H*. "rock macula" from Mushroom Island.

A female *H*. "rock macula" (Mushroom Island).

Habitat of members of the *chromogynos* complex: small rocks/sand interface at Bukoba.

Chamagati Island, *H. chilotes* and *H*. "short head chilotes".

A piebald male *H. chilotes*.

A territorial male *H. chilotes* in the aquarium.

ognized by the combination of a long head (head length 33 % of the standard length or more) with a relatively long lower jaw (34.7-41 % of the head length), small eyes (eye length between 21.2 and 22.5 % of the head length, 25.4 % according to Greenwood 1959a) and a prominent melanin pattern. Their lower jaws and dental arcades are slightly to strongly narrowed, their jaws isognathous, their outer teeth usually unicuspid, and the inner rows arranged in 2-4 rows. The dorsal head profile is shallow, and sometimes slightly concave. The lower jaw is 1.31 to 1.43 times as long as broad, the interorbital width with 21.3-21.8 % (to 23.8 % according to Greenwood) of the head length very narrow. The chest scales are small and deeply embedded and there are between 5 and 6 vertical bars on the flanks. Both known species develop strongly lobed lips.

Haplochromis (Paralabidochromis) chilotes (Blgr.) 1911 is probably the most unmistakable species among the rock-dwelling cichlids of Lake Victoria. It is characterized by a long, pointed snout, narrow tooth arcades with rather stout unicuspid outer teeth that are somewhat recurved, two to four inner tooth rows, lips that are usually produced into small to very big lobes, and a conspicuous chessboard pattern. *H. (P.) chilotes* is one of the most widely distributed species among the rock-dwelling Lake Victoria cichlids and the matrix species of this complex. We know it from 16 localities in the surveyed area. It is furthermore known from several places in northern Lake Victoria (Greenwood 1959a). However, its distribution is less even than that of other widely distributed *Mbipi* species, such as *H. (P.)* "rockkribensis" or *H . (Xystichromis)* "copper black", and *H. (P.) chilotes* is absent from many sampled localities. In spite of its unmistakable anatomical appearance, some doubts remain about the identification of the fishes from southern Lake Victoria (see below).

In spite of geographical variation in coloration among populations, we consider all forms, known from the surveyed area, as belonging to a single species, because never more than one colour type lives at any one place, and because differences in male breeding dress are little and not correlated with anatomical or ecological differences. Geographical variation concerns predominantly the ground coloration, which is in most populations yellowish grey, in the fishes from Chamagati Island deep yellow (in particularly lips and head underside), in those from Miandere Island almost orange, and in those from Senga Point pale grey with pinkish lips. Males usually have light blueish flanks, tending to greenish on the caudal peduncle, a more or less orange coloured chest, a blue dorsal fin with red streaks in the soft part, a greyish red to red caudal fin, and a pale reddish anal fin. The intensity and extension of the orange chest coloration is again subject to geographical variation. The coloration of the flanks is superimposed by a chessboard pattern, the longitudinal bands of which fade away during reproductive and territorial activity.

However, Greenwood (1959a) described for *H. (P.) chilotes* from northern Lake Victoria an entirely different male coloration. The ground colour of his fishes was greyish-black or black with a black dorsal fin that had red lappets and red maculae between the branched rays. The caudal fin was black basally, and light yellow or hyaline distally, the anal yellow or hyaline, with reddish-yellow egg dummies. If this coloration is indeed typical for the northern populations, then populations at the eastern and western lake shores have to be investigated, before it can be said with certainty, whether the southern and northern forms belong to the same species. Recently *H. (P.) chilotes* from Uganda was imported to Europe by aquarium fish importers. These fishes resemble in coloration the southern populations (see photo in Kirner 1994). Unfortunately neither the exact geographical origin of these, nor of Greenwood's black males is known.

Females carry a prominent chessboard pattern on light silvery- to yellowish-grey, yellow, or grey-orange background. Females at Chamagati Island are almost as bright yellow as *H. (P.)* "rockkribensis" females. A rare piebald colour morph exists in several populations of *H. (P.) chilotes* (Greenwood 1959a, 1974, Seehausen & Bouton 1996). We collected alive one individual from Zue Island (Speke Gulf), bearing black blotches on a silvery whitish background (see photo). More recently I observed two piebald individuals at Ruti Island, a brooding female at 8 m water depth, and a subadult at 14 m depth. Under the light conditions at those depths, these fishes appeared bright white with prominent big black blotches, dispersed over the entire body.

Greenwood (1959a) described considerable variation in the expression of the lip lobes, as well as in head length, and lower jaw length. In contrast to his observations, we observed very little intra- and interpopulational variation in this respect. We have never encountered adult individuals without or with only weakly lobed lips. However, I suspect that Greenwood had individuals in his sample that belonged to another, as yet undescribed species, *H. (P.)* "short head chilotes" (see below). Already small juveniles of *H. (P.) chilotes* are readily recognized by virtue of their narrow, pointed beaklike snout. In our aquarium raised stocks, the lips start do swell at a size of about 70 mm standard length.

H. (P.) chilotes inhabits predominantly gently sloping rock shores, and is abundant only at places with very small rock boulders. It occurs in low population densities also at moderately steep shores with medium sized rock boulders (e.g. in the Mwanza Gulf), but is absent from steeply sloping shores with very big rock boulders. If, however, at steeply sloping places the substrate at the foot of the steep rock cliffs is also rocky, *H. (P.) chilotes* can be found in those deep waters. Such a situation exists at Ruti Island, where the lobed lip cichlid can be observed rather frequently at water depths between 8 and 14 m. Sometimes, however, the population density or the complete absence of *H. (P.) chilotes* from a particular place is not that readily explained by habitat characteristics. At islands with very small rock boulders we observed *H. (P.) chilotes* moving in small groups at water depths ranging from less than 1 to at least 2.5 m. At other islands with medium sized boulders, they lead a cryptic way of life in crevices between rocks, from the shallow water down to greater depths. Greenwood (1959a) found *H. (P.) chilotes* not only over rocks, but also over sand in the northern parts of the lake. F. Witte (pers. comm.) made similar observations in the Mwanza area of the southern lake. If these were not just occasional invaders of sand bottom habitats, then the species must have lost, after the Nile perch upsurge, a part of its former range of habitats. In seine nets pulled over sand bottoms at many places, we only once had a *H. (P.) chilotes*, and that was directly adjacent to rocks. Greenwood seemed to observe that this species would be restricted to sheltered bays and gulfs. This is certainly not the case. It frequently inhabits fully exposed places (e.g. the offshore Miandere, Makobe and Ruti Islands), probably even more often than sheltered ones.

The lobed lips in *H. (P.) chilotes*, and in lobed lip cichlids from other lakes, are thought to play a role in feeding. Their actual function, however, is disputed (e.g. Greenwood 1974, Fryer & Iles 1972). *H. (P.) chilotes* feeds primarily on insect larvae that are associated with epilithic *Aufwuchs*, mainly on may fly (Ephemeroptera) larvae. Out of five males from Chamagati Island and two females and one male from Makobe Island that we examined, three had eaten predominantly may fly larvae, one may fly and chironomid larvae to equal parts, two predominantly chironomids, and two filamentous blue-green algae. The latter two individuals, however, had very little food in their stomachs, and also all others had ingested some algae, indicating that algae are not the target items but ingested incidentally when insects are removed from the rocks. Fishes that have only some algae in their almost empty stomachs, probably missed the target insect when pulling their lips over a rock. While pulling and scraping its prey from the rocks, *H. (P.)*

H. "short head chilotes" and *H. chilotes* at Makobe island.

A male *H.* "short head chilotes" (Makobe).

A female *H.* "short head chilotes".

H. cf. chromogynos from Zue Island.

Guano-covered rocks at Ruti Island.

chilotes presses its big lips against the rocks, as aquarium observations have learned (Seehausen 1993). It searches its prey predominantly on the underside of rocks and in gaps between them. These are the preferred whereabouts of may fly larvae. To reach there, a fish turns sidewards before entering. In the aquarium *H. (P.) chilotes* is frequently observed digging for prey under slightly overhanging rocks.

Females of *H. (P.) chilotes* are more frequently encountered than males, while it is the other way around in almost all other species of *Mbipi.* This may hint at some, as yet not known difference in ecology. *H. (P.) chilotes* seems for instance, to be less territorial than most other *Mbipi*. It usually lives sympatrically with other species of Chessboard *Mbipi*: with most species of the *H. (P.)* "rockpicker" and the *H. (P.)* "rockkribensis" complexes, with several species of the *H. (P.) chromogynos* complex and at several places with the second lobed lip cichlid of Lake Victoria, *H. (P.)* "short head chilotes".

Haplochromis (Paralabidochromis) **"short head chilotes"** is maybe the most remarkable of the many new discoveries at rocky shores. The species, on first glance, closely resembles *H. (P.) chilotes,* because it has very similarly lobed lips, and an equally prominent chessboard melanin pattern on a silvery grey background. However, it differs considerably from that species in a number of characters. It has a much shorter head, and relative to the head length, much shorter jaws (table 3). Hence the name "short head chilotes". Moreover, it differs from *H. (P.) chilotes* in the coloration of both sexes. In the Sengerema region, and in particular at Chamagati Island, *H. (P.) chilotes* has a prominent yellow ground colour (see photo). In contrast, *H. (P.)* "short head chilotes" is at the same places silvery whitish, without any trace of yellow. The only known male in breeding dress, caught at Makobe Island, differs from *H. (P.) chilotes* males from the same island and habitat, by having operculum, chest and belly dull coppery red. The remaining flanks are yellowish with a pinkish flush, the area above the anal fin basis is blue-green. The orange-red chest area of *H. (P.) chilotes* is smaller then the coppery area of this male, and is in males from Makobe Island hardly present at all. Finally does *H. (P.)* "short head chilotes" have six vertical bars on the flanks, versus 4-5 in *H. (P.) chilotes*.

Among the four individuals that we collected of "short head chilotes", two have fully lobed lips, one has an only slightly lobed lower lip, and a non-lobed but thickened upper lip, and one has it the other way around. Greenwood (1959a) reported considerable variability of *H. (P.) chilotes* with respect to lip form, head length and lower jaw length. Though he wrote that his sample as a whole shows a complete intergradation of lip, jaw and dental characters (the reason for him to consider the fishes to represent a single species), he gives ranges and means of measurements for two types, lobe-lipped and non-lobe-lipped fishes. Those of his non-lobe-lipped group are very similar to our measurements of "short head chilotes", while those of his lobe-lipped group exceed the range of our measurements of *chilotes* (compare tables 3 and 4). I suspect, that Greenwood had some "short head chilotes" in his apparent *chilotes* sample. Since he sorted the phenotypes according to lip size, and small or non-lobed lips are more common in "short head chilotes" than in *chilotes*, his non-lobe-lipped group would have largely consisted of *H. (P.)* "short head chilotes". His lobe-lipped group would have consisted of both species. If this is true, "short head chilotes" would be much more widely distributed, than is currently known. Apart from the lip shape, and the prominent melanin pattern, *H. (P.)* "short head chilotes" is anatomically closer to the species of the *H. (P.) chromogynos* complex, than to *H. (P.) chilotes*.

Basically nothing is known yet about the ecology of "short head chilotes". All three record localities have moderate to very gentle slopes, and medium sized to small rock boulders. At Chamagati Island we found *H. (P.)* "short head chilotes" at the very gently sloping shore at water depths between 1.5 and 3 m, sympatrically with *H. (P.) chilotes*, *H. (P.)* "blue rockpicker", *H. (P.)* "yellow rockpicker", and *H. (P.)* "rockkribensis". At the Sengerema mainland shore we caught one female in even shallower water of less than a metres depth. Finally, we caught a big male at Makobe Island at 5-6 m depth, again in sympatry with the above mentioned four other chessboard species, plus *H. (P.)* "short snout scraper". Like above described for *H. (P.) chilotes,* we encountered also of "short head chilotes" more females than males, contrasting with the ratio known from most other *Mbipi* in Lake Victoria.

The ***Haplochromis (Paralabidochromis) chromogynos*** complex

Within the Chessboard *Mbipi* the members of this species complex are recognized by the combination of a long head (head length more than 33% of the standard length), with a relatively long lower jaw* [footnote: *values of Greenwood (1959a) in parentheses if deviating from mine] (35 [32.5] to 38% of the head length), relatively big eyes (eye length between 24 and 27.6[28.6] % of the head length) and a faint melanin pattern. Their lower jaws and dental arcades are narrow, though not as narrow as those of *H. (P.) chilotes*. Most species have rather widely spaced, slender and somewhat recurved unicuspid teeth in the outer rows, and 3 to 5 inner rows of teeth that stand more or less upright. One species has bicuspid outer teeth and only two inner rows. The dorsal head profile slopes gently to moderately steep and is straight or slightly concave. The jaws are usually isognathous (one species with a retrognathous lower jaw). The lower jaw is always longer than broad, with a length/width ratio between 1.26 and 1.53. The interorbital width can be as narrow as in the *H. (P.) chilotes* complex, but also much wider (20.6-25.4[27.5] % of the head length). The chest scales are size reduced and deeply embedded in three of the four known rock-dwelling populations and there are usually six vertical bars on the flanks.

Only one species is described. We know from southeastern Lake Victoria currently four populations of *chromogynos*-like cichlids. All inhabit geographically narrowly restricted areas, and all are anatomically different from each other. One may represent the real *H. (P.) chromogynos* but the others represent very probably undescribed species. However, due to their rarity, they are poorly studied. The scattered distribution of this species complex almost certainly is the result of recent extinction of populations.

Haplochromis (Paralabidochromis) chromogynos Greenwood 1959 is known from several regions of Lake Victoria (Greenwood 1959). A form that may be this species was frequently caught in the Mwanza Gulf before the Nile perch upsurge (Witte et al. 1992). It inhabited rocky and sand bottoms in the Nyegezi and Butimba Bays but has not been seen any more after 1982 (Witte et al. 1992). None of the forms that we found in the 1990s at rocky and pebble shores fits Greenwood's description of *H. (P.) chromogynos* fully. One form is close to it in body and head shape but differs in dentition. This ***H. (P.) cf. chromogynos*** is known only from Zue Island in the northern Speke Gulf. It has in both jaws five rows of inner teeth, while *H. (P.) chromogynos,* according to Greenwood, should have three (rarely two or four). It is extremely rare at Zue Island and lives sympatrically with the other *Paralabidochromis* species *H. (P.) chilotes*, *H. (P.)* "Zue rockpicker" and *H. (P.)* "rockkribensis" at about 4 m water depth over a gently sloping small rock and pebble substratum. I am not sure that there exists actually a viable population. Greenwood (1959) described *H. (P.) chromogynos* as a rare example of polychromatism, in which all females belong to the piebald morph but all males to the normal coloured morph. The only individual that we caught at Zue Island is a female of the piebald morph, having black blotches on a clear white ground. This piebald coloration is

A male *H*. "fleshy lips" from Mponze Point.

A female *H*. "fleshy lips" from Mponze Point.

very similar to that occurring in a morph of *H. (Neochromis)* "blue scraper", and differs from that observed in *H. (P.) chilotes* at Zue Island (black blotches on more silvery whitish ground). *H. (P.) cf. chromogynos* has slender, rather fine, widely but regularly spaced, acutely pointed, and recurved unicuspid teeth in the outer tooth rows, and unicuspid

H. "long teeth" from Matwinki Island.

teeth also in the inner rows, similar to what Greenwood described for this species. Its lips are thickened, particularly the upper one and covered by a thick mucus layer.

At Irondo Point, near the entrance to the Mwanza Gulf, we found another representative of *H. (P.) chromogynos*-like cichlids. Also this one inhabits a rather gently sloping shore, where it lives in an extensive rock garden with interspersed patches of sandy bottom. It has a longer head than *H. (P.) chromogynos*, and differs in dentition from the latter, and from all other forms that are known in this complex: The outer tooth rows are in both jaws composed of less slender bicuspid teeth, with a well developed minor cusp and a slightly recurved major cusp, that is in most cases strongly outworn. Moreover, there are only two rows of small inner teeth in each jaw. Finally, are lower jaw and dental arcade slightly pointed, and not rounded, as in all other forms. The lips are hardly thickened, and are covered by just a thin mucus layer anteriorly and anterolaterally. We caught only one fish (a big male) yet, which was rather dull grey-green in coloration. The considerable differences in jaw shape and dentition make it most probable that this population represents another species, for the time being called ***Haplochromis (Paralabidochromis)* "pointed jaw chromogynos"**. Its chest scales are small and deeply embedded.

Two further populations of *H. (P.) chromogynos*-like cichlids differ from *H. (P.) chromogynos* as described by Greenwood, from our *H. (P.) cf. chromogynos,* and from *H. (P.)* "pointed jaw chromogynos" by a narrower head, and a longer and narrower lower jaw. One of them ***Haplochromis (Paralabidochromis)* "fleshy lips"** inhabits a small rock boulder and sand-rock mixed habitat at Mponze Point in the southwestern Speke Gulf. Its population density was, when we discovered the species in 1993, much higher than in the aforementioned two populations. It was even the second most abundant species at Mponze Point, after *H. (Xystichromis)* "copper black". Unfortunately, we could not find it there any more when we searched for it in 1996. It inhabited a very gently sloping shore at water depths from less than half a metre to at least 1.5 m. We collected both sexes in approximately equal numbers, a rare situation among *Mbipi*. Males of "fleshy lips" are dark blue-grey on head and flanks, have a blueish dorsal fin with red lappets and red maculae among the branched rays, a caudal fin that is greyish in the upper, red in the lower half, and a red anal fin with often quite large, dark yellow egg dummies. Males develop swollen, and sometimes very slightly lobed lips with a thick mucus cover all over, hence the name "fleshy lips". Females are golden yellow with red streaks and maculae in dorsal and caudal fin and frequently exhibit distinct orange yellow egg dummies with a white outer ring. Their lips are less thickened than those of the males. Both sexes have about six vertical bars on the flanks. *H. (P.)* "fleshy lips" has slightly recurved unicuspid teeth in the outer rows, which are usually strongly outworn, and less slender than in *H. (P.) cf. chromogynos* and *H. (P.)* "long teeth". Its inner teeth are long and unicuspid or weakly tricuspid as well, and its chest scales are bigger, and not as deeply embedded as in the other *chromogynos*-like forms and most other *Mbipi*.

The second population with a narrow head, ***Haplochromis (Paralabidochromis)* "long teeth"** lives at Matwinki (Nyahihi) Island in the Sengerema region. It differs from *H. (P.)* "fleshy lips" by its finer, and acutely pointed outer teeth that are strongly recurved in the upper jaw, and more widely spaced than in *H. (P.) cf. chromogynos*, by hardly thickened lips that are free of mucus, by a more concave dorsal head profile, and by a different chest squamation with smaller and more deeply embedded scales. Its habitat is a very gently sloping small boulder and pebble shore. Its population density must be extremely low. We caught two individuals, one in 1993, the other one in 1995, at exactly the same place among small boulders and stones, at only 0.8-1.2 m water depth. They lived sympatrically with the *Paralabidochromis* species *H. (P.)* "yellow rockpicker" and *H. (P.)* "rockkribensis", and with the anatomically similar *H. (Psammochromis) cf. saxicola*. From the latter species, "long teeth" can be distinguished by a narrower snout, the incurved dorsal head profile, and by dentition. *Psammochromis* of the size of "long teeth" still have many bicuspid teeth in the outer tooth rows, and deeper embedded inner tooth rows. One of the two so far collected individuals of *H. (P.)* "long teeth" is a black and white piebald female.

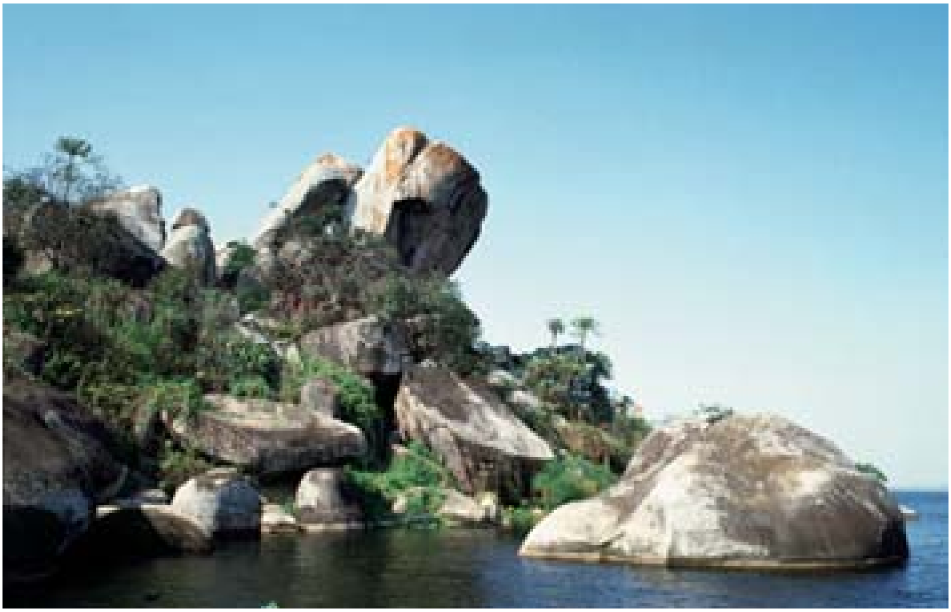
Rock-dwelling cichlid species of other lineages

Shallow heads and narrow jaws — the *Psammochromis* lineage

Members of this group are rather large growing insect and mollusc eating species, that are anatomically not much derived from the generalized *Astatotilapia* like haplochromine. Greenwood defines the genus *Psammochromis* Greenwood 1980 as *relatively slender to moderately deep bodied haplochromines with a characteristic physiognomy, created by the combination of thickened lips, a straight, moderately steep dorsal head profile and a horizontal or but slightly oblique mouth. The outer jaw teeth are tall and slender, unequally bicuspid and unicuspid, their crowns recurved and either compressed or finely acuminate in cross section. The tall and slender inner teeth are usually implanted so as to lie almost horizontally, are unicuspid in larger fish, and deeply embedded in oral mucosa, so that they often appear small on first glance. The inner teeth being arranged in 2-4 (rarely 5) rows, there is a tendency to an increased number of tooth rows compared to the generalized* Astatotilapia *like condition. As a consequence of a peculiar anatomy of the dentary (lower jaw bone), the outer tooth row in the lower jaw describes anteriorly a ventral inflection, so that the tips of the outer teeth are on one level with the much shorter inner teeth.* This Greenwood (1980) considers "the most trenchant and diagnostic synapomorphy (derived character shared by the members of a lineage) linking members of the *Psammochromis* lineage", though it is shared with the species of the *Ptyochromis* and *Macropleurodus* lineages, and is, less prominently, also in the *Paralabidochromis* lineage present. *The mouth lies horizontally or but slightly oblique, the dentary (teeth carrying lower jaw bone) is very shallow, creating a slender and attenuated impression of the jaws. The scales on the chest are in the hard bottom dwellers (see below) distinctly smaller and more deeply embedded than those on flanks and belly. Several species usually bear outworn outer teeth with abraded crowns, giving the teeth a bluntly incisiform appearance.*

At the rocky shores in southeastern Lake Victoria we found at least eight haplochromine species that fit Greenwood's definition of *Psammochromis*. Three of them are described, the others are new, undescribed species. Apart from above mentioned characters, they share a relatively long head (32.2-35.9% of the standard length), relatively long lower jaws (37.3-43.9% of the head length), a medium to large lower jaw length/width ratio (1.3-1.7), and a relatively narrow head. All have size reduced chest scales that are deeper embedded than those on the body. Species of this complex can be confused with species of the *H. (Paralabidochromis) chromogynos* complex, as well as with small piscivores. From the first group, they differ by a usually longer lower jaw, a higher jaw length/width ratio, and by a stronger ventral inflection of the outer teeth in the lower jaw. Furthermore are the inner teeth in *Paralabidochromis* usually not long and slender. From fish eating species, members of the *Psammochromis* lineage differ again by the inflection of the lower jaw teeth, by shorter lower jaws and usually less acutely pointed teeth in the outer tooth row.

Similar to the *Paralabidochromis* lineage, and different from the lineages of "Vertical bar *Mbipi*", the *Psammochromis* lineage is not confined to rock bottoms. *H. (P.) riponianus*, *H. (P.) saxicola* and *H. (P.) aelocephalus* have been described from rock, shingle and sand bottoms (Greenwood 1959a, 1960, Witte et al. 1992), *H. (P.) acidens* from macrophyte vegetation, and *H. (P.) cassius* from mud and sand bot-


The rocky shore of Ascari Island.


A male *H. riponianus* from Senga Point.


A female *H. riponianus* (Sozihe Island).


A freshly caught male *H. riponianus* at Igombe Island.

A male *H. cf saxicola* (Sozihe Island).

A female *H. cf saxicola* from Chamagati Island.

toms (Greenwood 1967, Greenwood & Barel 1978, Witte et al. 1992). Apart from the three described hard bottom dwelling species, we found five new species that, with the currently available information, qualify as *Psammochromis*, but may be restricted to rocky substrates. The occurrence or absence of *Psammochromis* in rocky habitats is sometimes not easily explained by habitat characteristics. For instance Zue Island in the Speke Gulf, that is in terms of habitat and ecological composition of its cichlid community very similar to the Sengerema islands Chamagati and Matwinki, lacks any insectivore of the *Psammochromis*-lineage that are very typical for the latter islands. The species of the *Psammochromis* lineage feed predominantly on large insect larvae (may and caddis fly larvae), ostracods and small bivalves (sphaeriids). Some species eat also snails.

Rock-restricted and non-rock-restricted *Psammochromis* have a melanin pattern that is similar to that of the Chessboard *Mbipi*. It consists of, sometimes rather irregularly set vertical bars, superimposed by mid lateral and dorsal lateral stripes that are usually dissolved into elongate blotches. The most prominent mid lateral blotch extends from the gill cover to the middle of the flank, ending between the tip of the pectoral fin and the height of the anal fin insertion. A second, less prominent blotch can stretch along the caudal peduncle. The dorsal lateral stripe can be dissolved into blotches of varying size and position but is usually most prominent along the central two thirds of the dorsal fin. I call this melanin pattern a "broken chessboard".

Greenwood (1980, 1981) considered *Psammochromis* to be part of a large supposedly monophyletic complex, the *Psammochromis-Macropleurodus* superlineage which, according to him, includes, apart from *Psammochromis*, all described oral shelling molluscivores of Lake Victoria and *Paralabidochromis*. However, Lippitsch (1993), who studied scale and squamation characters of various Lake Victoria haplochromines, suggests that *Psammochromis* is neither a monophyletic lineage, nor belonging into the close relationship of the oral shelling molluscivores.

Haplochromis (Psammochromis) riponianus (Blgr.) 1911 is known from many sand bottoms and vegetation zones, and from some rocky habitats in southern Lake Victoria, as well as from the northern parts of the lake (Greenwood 1960, Witte et al. 1992, Kaufman & Ochumba 1993). However, since populations differ in coloration and at least one similar undescribed species exists, a revision of *H. (P.) riponianus* is desirable. Males active in reproduction, can be light metallic blue on the flanks with a light underside. Similarly light blue is in such fishes the dorsal fin that bears a dark grey margin and red lappets. The caudal fin is red distally, and the anal fin is light red with small egg dummies. In other populations males are darker blue-grey to green-grey with similar, but also darker fin coloration (Van Oijen 1978). In many populations the pelvic fins are black in the spinous, red in the branched ray part. Sexually quiescent males are silvery grey with some blue flush on the flanks. Females are more or less intensely golden yellowish, and carry, like the males, six or seven vertical bars on the flanks. Individuals collected by seine net over sand are usually lighter coloured than those collected over rocks or among vegetation. However, compared to other rock-dwelling cichlids, *H. (P.) riponianus* is generally light coloured, similar to many sand-dwelling species.

H. (P.) riponianus feeds predominantly on large insect larvae (may fly and caddis fly larvae) but to lesser extends also on bivalves and snails (Greenwood 1960). It usually has somewhat enlarged pharyngeal jaws, provided with strong teeth, that tend to be submolariform and/or molariform, suitable for crushing cases of caddis fly larvae and mollusc shells. We found *H. (P.) riponianus* at several places over sand bottom (mostly in not fully wave exposed areas), as well as over sand-rock mixed substrates and habitat interfaces. Less frequently we encountered it between 0.5 and 2.5 m depth over pure rock substratum, where the latter slopes gently and consists of small boulders. Steeply sloping rocky habitats in the Mwanza Gulf are inhabited by *riponianus*-like fishes that differ from this species in coloration and anatomy, and most likely represent a separate, undescribed species.

Very similar to *H. (P.) riponianus* is ***Haplochromis (Psammochromis) saxicola*** Greenwood 1960. It differs from *H. (P.) riponianus* in male coloration and by virtue of more slender pharyngeal bones that, in most individuals, do not carry molariform teeth. Furthermore the lower jaw is frequently longer in *H. (P.) saxicola* than in *H. (P.) riponianus*, the oral teeth are arranged in fewer rows, and those in the outer row become earlier unicuspid. Reproductively active males are, according to Greenwood (1960) dark grey-green, some scales on the flanks having golden centres, chest and branchyostegal membrane are black, and there is a coppery-red flush on the opercula and flanks. The dorsal fin is dark, with red lappets and maculae, the caudal fin is blue-grey with red margin, and the anal fin is blue-grey with pink flush and bright yellow egg dummies. The pelvic fins are black. Quiescent males, as well as females closely resemble those of *H. (P.) riponianus*.

Several populations of *Psammochromis* in southeastern Lake Victoria agree very closely with Greenwood's description of *H. (P.) saxicola* but have shorter heads and lower jaws than Greenwood's fishes. Greenwood used exclusively individuals from the northern lake shores for his description. Since also our southern *H. (P.) riponianus* have shorter lower jaws than his northern ones, the difference between northern and southern fishes may reflect an across-species impact of an ecological factor, correlated with geography. Like in other cases, mentioned before, final clarity, whether the southern and northern populations belong to the same species or not, can also for *H. (P.) saxicola* be achieved only after the eastern and western shores of Lake Victoria have been investigated. In agreement with Greenwood's description, even the biggest southern *H. (P.) saxicola* have rather slender pharyngeal bones, bearing only slightly enlarged, non-molariform teeth, and have fewer oral tooth rows than *H. (P.) riponianus*. In both species, the teeth are frequently strongly outworn, the crowns abrased. Southern *H. (P.) saxicola* have five to six vertical bars on their flanks.

We found *H. (P.) saxicola* at three places. At two of them (Chamagati and Matwinki Islands), the habitat is a very gently sloping shore with small rock boulders and rubble. The species occurs here already immediately inshore in very shallow water. Subadults are found in waters of less than 0.5 m depth, full adults at 1 to at least 2 m depth. At some places at Chamagati Island, in waters of less than 1 m depth over rubble, *H. (P.) saxicola* is quite abundant. We found an approximately equal sex ratio in our catches, which is a rare feature among rock-dwelling Lake Victoria haplochromines (but see under *H. (Paralabidochromis) chilotes* complex). At Sozihe Island in the eastern Speke Gulf, *H. (P.) cf. saxicola* (I have not yet measured the fishes to confirm the identification) is restricted to rather gently sloping areas with small boulders and lives there between 0.5 and 2.5 m water depth. According to Greenwood (1960), this species eats predominantly insect larvae (chironomids and may fly larvae) and ostracods, less commonly also snails. In the stomach and intestine of one individual from Matwinki Island we found may fly larvae, caddis fly larvae, chironomid larvae and ostracods to about equal parts, as well as crushed shells of some rather big sphaeriid bivalves.

At Chamagati Island, *H. (P.) saxicola* lives sympatrically with two similar species, an unidentified *Psammochromis* and *H. ("Astatotilapia")* "black long snout". At Matwinki Island it lives sympatrically with *H. (Paralabidochromis)* "long teeth", that has a similarly long and pointed snout. Finally, at Sozihe Island, it lives in sympatry with *H. (P.) riponianus*. From the unidentified *Psammochromis*, it differs by having a longer head, a more slender lower jaw, and a more pointed snout. From *H. ("A.")* "black long snout" it differs in size, male coloration and dentition, and from *H. (P.)* "long teeth" in lower jaw shape and dentition (see table 3).

An undescribed *Psammochromis* that is apparently confined to rock substrate, and is known only from moderately to steeply sloping shores of the central and northern Mwanza Gulf is ***Haplochromis (Psammochromis)*** **"rock riponianus"**. From both above described species it differs by virtue of a steeper dorsal head profile and a less pointed snout, from *H. (P.) riponianus* by fewer tooth rows. Males have grey-green flanks, very much like *H. (P.) saxicola*, sometimes with a distinct red flush all over. The dorsal fin is dark with red lappets and maculae between the branched rays, the caudal fin is grey with red margin, to almost entirely red, the anal fin is red, with orange coloured egg dummies. Unlike male *H. (P.) saxicola*, the males of this species have the soft part of the pelvic fins red, and only the spinous part black. In this respect, they resemble *H. (P.) riponianus*. There are six or seven vertical bars on the flanks. Females are darker brownish than those of the two previously discussed species.

H. (P.) "rock riponianus" lives at moderately steep and very steeply sloping rock shores that consist of medium sized to very big rock boulders. At such places it lives at water depths from 1 to 4 m. It is nowhere abundant and, like in other rock cichlids and unlike in the two above discussed *Psammochromis*, males are encountered clearly more often than fe-

A male *H.* "rock riponianus" from Shadi Rocks.

A male *H. aelocephalus* from Bihiru Island.

males. The habitat requirements of *H. (P.)* "rock-riponianus" seem to be similar to those of the anatomically and in male coloration very different *H. (P.) aelocephalus*, and the two species live sympatrically at least at Hippo Island in the northern Mwanza Gulf, possibly at more places. On superficial glance "rock-riponianus" can be mistaken for *H. (Xystichromis)* "copper black", with which it lives sympatrically at some places. Males of the latter, however, have entirely black rather than half red pelvic fins, and very different dentition.

Haplochromis (Psammochromis) aelocephalus Greenwood 1959 is the third described species of the *Psammochromis*-lineage that occurs in rocky habitats. Greenwood described it, like the other two species, exclusively from fishes collected along the northern, Ugandan lake shores. According to him, the species lives over sand and rock. We found *H. (P.) aelocephalus* at five localities in the southeastern lake. One population inhabits a sand-rock interface at the southern shore of the Bwiru Peninsula, the other four inhabit purely rocky habitats with moderate to very steep slopes in the central Mwanza Gulf, where they live as real crevice dwellers. I cannot rule out the possibility that the fishes from the two very different habitat types represent two different species. The males from the rocky islands are dark pinkish-grey all over. A smaller or bigger orange coloured area is situated behind the pectoral fin, followed by a large area, in which each scale has a blue-green iridescent centre, extending along the lower half of the flank

A female *H. aelocepahalus* from Bihiru Island.

A female *H.* "Ruti-Psammo" from Ruti Island.

A male *H.* "blue sharp snout" from Bwiru island.

to the caudal peduncle. This coloration is superimposed by five rather broad dark vertical bars. The dorsal fin is metallic purplish, with red lappets and streaks among the branched rays. The caudal fin is dark purplish-grey with red streaks and maculae; the anal fin is dark purplish-grey with bright orange egg dummies. Females are darker brown than those of the previously discussed *Psammochromis* species, and exhibit a slight purplish flush on the flanks. I do not know the male coloration of the population that inhabits a sand-rock interface.

Among all *Psammochromis* of the rocky shores, *H. (P.) aelocephalus* has the most peculiar head shape. The snout is even longer, and more acutely pointed than in the others. However, we never found individuals with strongly thickened or even lobed lips as described by Greenwood (1959). The fishes that we collected at Bihiru Island have a much smaller mean and maximum size than those from the Mwanza Gulf.

The dark coloration identifies *H. (P.) aelocephalus* as real rock-dwellers. Apart from the above mentioned individual, collected in a sand-rock mixed habitat, we found the species in crevices between rocks in immediately inshore waters of 1 to 3 m depth. At the less steeply sloping Hippo Island we found a very big male at about 5.5 m depth. *H. (P.) aelocephalus* occurs usually in low population densities but is the numerically dominant crevice-dweller at Bihiru Island. It deviates in habitat choice from the other rock-dwelling *Psammochromis*, which inhabit gently sloping small boulder shores, or steeper slopes outside of crevices.

Another morphologically peculiar species is ***Haplochromis (Psammochromis)* "Ruti-Psammo"**, which we collected at Ruti Island in the central Speke Gulf. To date we found only two females and could not find this distinct species anywhere else. The fish has a characteristic physiognomy, with a *Psammochromis* head shape, but a somewhat foreshortened snout, setting it anatomically apart from the other *Psammochromis* species. Otherwise it shares all above mentioned characters of the *Psammochromis* lineage, and in particularly a strong ventral inflection of the outer tooth row anteriorly in the lower jaw. Nothing is known yet about the ecology of this rare fish. Both individuals were caught somewhat offshore between 6 and 10 m water depth.

Just as little known as the latter species is also ***Haplochromis (Psammochromis)* "blue sharp snout"** from Bwiru Island, southwest of Ukerewe. It is a large growing species that differs from the other *Psammochromis* by a greater body depth and by a broader head. This causes its physiognomy to deviate slightly from that of the other species, its snout appears less attenuated. Its assignment to the *Psammochromis* lineage is provisional. We have collected only one male yet. Apart from the broader head and deeper body, it exhibits all the characters, typical for *Psammochromis*. It is dark metallic blue with similarly dark fins. The dorsal fin has orange-red lappets and streaks in its soft part, the caudal fin has a broad orange-red margin, and the anal fin has a pale whitish margin with orange flush and orange coloured egg dummies. The orange-red coloration of the fin margins contrasts sharply with the dark blue coloration of the fin bases and the body. We caught the fish at an exposed shore with medium sized boulders and moderately steep slope in 8-10 m deep waters. Thus, this species and *H. (P.)* "Ruti-Psammo" seem to live deeper than most other rock-dwelling *Psammochromis* species. The whitish anal fin margin may at those depths play the role in courtship that I described earlier for deepwater-dwelling species of the *H. nyererei* complex (*H.* "blue nyererei", *H.* "pink anal").

The deeper parts of rocky shores in the southwestern Speke Gulf are inhabited by a species with distinctly enlarged pharyngeal teeth, ***Haplochromis (Psammochromis)* "striped crusher"**. It seems to occupy in that region an ecological position similar to that of *H. (Labrochromis)* "stone" in the Mwanza Gulf. Apart from *Astatoreochromis alluaudi*, no anatomically specialized pharyngeal crushing snail eater is known from the rocky shores in the southern and western Speke Gulf. Thus, this representative of the predominantly insect eating *Psammochromis* lineage may have entered into a vacant niche. *H. (P.)* "striped crusher" is in every respect a typical *Psammochromis*. Its long and slender outer teeth are in the lower jaw strongly procumbent, and the outer tooth rows exhibit a distinct ventral inflection. The pharyngeal dentition of adult individuals is composed of submolariform teeth. The scales on the chest are size reduced and somewhat deeply embedded, though less so than in many other rock cichlids. This is a rather inconspicuously coloured species with rather little difference between the sexes. Both are greyish-brown with yellowish caudal, anal and pelvic fins. The dorsal fin has red lappets and, in the male, red streaks or maculae. Both sexes have some metallic blueish to greenish flush on the flanks that is in males usually somewhat more prominent. Both exhibit rather prominent broken longitudinal stripes, while the vertical bars of the "broken chessboard pattern" are much less distinct.

H. (P.) "striped crusher" inhabits the rather gentle slope of Makobe Island as well as the steeply sloping Ruti Island. It is at all places very rare. Like *H. (Labrochromis)* "stone" (see below) it usually lives in sympatry with *Astatoreochromis alluaudi*, but the two snail eaters are ecologically segregated by depth. At Makobe Island, "striped crusher" lives offshore at depths beyond 4 m, while *A. alluaudi* lives predominantly in shallower waters. At Ruti Island, "striped crusher" inhabits the only gently sloping small boulder habitat at the foot of the huge, steep rocks, at 10 m depth and beyond that, while *A. alluaudi* again lives at lesser depths. A male from Igombe Island, whose stomach we checked, had eaten predominantly snails and ostracods, and smaller amounts of caddis fly and chironomid larvae. Surprisingly we did not find any shell fragments among the heaps of snail soft tissue. This suggests that the fish shelled, rather than crushed its prey. The strongly procumbent, long and slender outer teeth may serve this purpose, similar to those of *Ptyochromis* species (see page 190ff). *H. (P.)* "striped crusher" is one of the few rock-dwelling haplochromines, in which females are more commonly encountered than males.

H. "striped crusher" lives in sympatry with *H. (P.) riponianus* at Makobe and Igombe Islands, but occupies a different microhabitat. It differs from that species most obviously in coloration. From the anatomically specialized snail crusher *H. (Labrochromis)* "stone", *H. (P.)* "striped crusher" differs in body shape, oral and pharyngeal jaw dentition, and coloration. It is less deep bodied, has a narrower head, a less steep dorsal head profile, and a narrower, more attenuated snout. The head does not have the heavy appearance, that is typical for *H. (L.)* "stone" and the *Labrochromis* lineage in general. A trenchant difference lies in the shape of the outer teeth, which are in *H. (L.)* "stone" much shorter, stouter, and implanted in an upright position. The vertical bars on the flanks of "striped crusher" are not as broad as those of "stone", and the latter does not exhibit the broken longitudinal stripes. Sympatry of the two species seems to be rare and is known only from Hippo Island in the northern Mwanza Gulf, where "stone" is frequently encountered in crevices among inshore rocks, while we caught "striped crusher" only once, about 10 m off shore in deeper water. *H. (P.)* "striped crusher" has never been recorded further south in the Mwanza Gulf and is replaced by other mollusc crushers in the northern Speke Gulf.

Was "striped crusher", within the anatomical range of *Psammochromis*, the one that is most close to the anatomically specialized pharyngeal crushers, so is ***Haplochromis (Psammochromis)*** **"red zebra"** anatomically close to the specialized oral shellers of the *Ptyochromis* lineage. This very colourful species is known from the Mwanza Gulf entrance and the mainland coast west of it, as well as from Ukerewe (Nansio Bay). Quite some anatomical variation exists among individuals from different places that can, however,

A male *H*. "red zebra" from the Mwanza Gulf entrance.

H. "striped crusher" from Ruti Island.

not yet be evaluated because only one or two individuals are known from each locality. *H. (P.)* "red zebra" has rather typical *Psammochromis* shape with a straight dorsal head profile and a snout, that is long and attenuated, though not as long as in the described *Psammochromis* species. It possesses all characters, used by Greenwood to define *Psammochromis*. However, slightly divergent from the typical *Psammochromis* condition, the inner tooth rows in the upper jaw of fishes from Ukerewe Island are arranged so as to form a broad band anteriorly in the jaw, reminiscent of the condition in the *Ptyochromis* lineage. Again similar to the condition in some species of the latter lineage, the lower jaw in some individuals of "red zebra" is retrognathous.

A male *H.* "yellow giant" from Mponze Point.

Only males are known yet of *H. (P.)* "red zebra". They carry usually seven narrow dark vertical bars on yellowish red to bright red flanks. The dorsal fin is anteriorly blue, posteriorly blood red or with such coloured streaks and maculae. The caudal fin is bright red, the anal fin pale reddish with yellow egg dummies. The pectoral fins are either entirely black, or half black (spinous part) and half red (soft part). The outer teeth in the lower jaw are long, slender and strongly procumbent. The scales on the chest are small and deeply embedded like in the

The rocky shore of Bihiru Island.

majority of rock restricted cichlids.

At all four record localities, the species is extremely rare. Its habitats are gentle, and moderately steeply sloping shores, with medium sized rock boulders. It lives slightly offshore at depths beyond 3 m. One male from Ukerewe, that we examined, had the first part of its intestine packed with dark grey snail flesh, the last part with may fly larvae. Snail shell fragments were not present, implying that the fish shelled its snail prey. At several places, *H. (P.)* "red zebra" lives sympatrically with *H. (P.)* "rockriponianus", and with the anatomically more specialized snail sheller *H. (Ptyochromis) xenognathus*. At Hippo Island it lives in sympatry furthermore with *H. (P.)* "striped crusher" and *H. (P.) aelocephalus*. From all four it differs in anatomy and coloration. In coloration "red zebra" superficially resembles *H. nyererei*, with whom it lives in sympatry at Hippo Island. It differs from the latter anatomically, and by having the red extending over the entire flanks, while red in *H. nyerere*i is restricted to the dorsum and upper flanks.

***Haplochromis (?)* "yellow giant"** is a rare, large growing species that I cannot unambiguously assign to any of the lineages Greenwood described. However, it shares a number of characters with the species of the *Psammochromis* lineage, and is anatomically probably closer to them than to any other lineage. Its dorsal head profile is steeper than in typical *Psammochromis*. Its outer teeth are less slender than those of typical *Psammochromis*; the outer tooth row is anteriorly in the lower jaw but slightly ventrally inflected, and thus, the teeth are but weakly procumbent. The teeth in the inner rows stand upright, rather than being more or less horizontally implanted; and they are not deeply embedded in oral mucosa. Some individuals have the teeth on the lower pharyngeal bone in the median rows enlarged, in others they are just slightly coarser than the other pharyngeal teeth. Males have bright yellow flanks and a more blue-grey dorsum. The dorsal fin is blueish with, among the branched rays, a characteristic pattern of blood red streaks, that dissolve into maculae in the distal half of the fin. The blueish caudal fin has a similar blood red pattern of streaks and maculae, and the anal fin is pale blue-grey with reddish flush distally and yellow egg dummies. There are six to seven vertical bars on the flanks and broken horizontal lines.

H. "yellow giant" lives at very gently sloping to moderately steep shores with small to medium sized boulders, and over sand-rock mixed substrates. We found it also in a seine net that was pulled over sand bottom. Thus, the species seems not to be restricted to rocky substrates. It is that rare everywhere that not much can be said about its depth distribution. At Vesi Islands we caught two males at 3 and 4 m water depth. At Mponze Point we observed big males in water, less than 1 m deep. This is rather unusual for big insect eating haplochromines. The feeding habits of "yellow giant" might be in line with those of some typical *Psammochromis*. A big male with enlarged pharyngeal teeth from Vesi Islands had its intestine filled to 50% with ostracods, 45% with crushed shells of sphaeriid bivalves, and with a few larvae of chironomids and may flies. The species' geographical distribution is similar to that of *H. (P.)* "striped crusher". The two differ distinctly in dentition and male coloration, and seem to be at least partly segregated by habitat.

Hook-teeth — the *Ptyochromis* lineage of snail shellers

Snail eating cichlids are in Lake Victoria more species rich than in the other African Great Lakes. Two basically different feeding strategies have evolved. One group, with their specialized oral dentition, pulls the soft body of the snail out from the shell, or crushes the shell between the oral teeth. These are the so called oral shellers which are described in this chapter. The other group crushes the shells of snails between enlarged pharyngeal jaws, provided with broad molariform teeth, the "pharyngeal mill". These are the so called pharyngeal crushers, described in the next chapter.

Both groups are dealt with in some detail by Greenwood 1974.

About 23 species of snail eating cichlids are known from Lake Victoria that shell or crush their prey with their oral jaws, rather than between the pharyngeal jaws (Greenwood 1956b, 1957, Witte et al. 1992, Kaufman & Ochumba 1993, Seehausen 1993, Kaufman & Seehausen 1995). The majority of these share a particular head anatomy, and oral dentition with recurved unicuspid (or weakly bicuspid) teeth in the outer tooth row and broad rows of usually unicuspid inner teeth. For these species Greenwood (1980) described the genus *Ptyochromis*. I treat them here as species of the *Ptyochromis* lineage. Greenwood defined the lineage as *haplochromines with a dorsal head profile ranging from straight and steeply sloping to strongly decurved, a small, more or less horizontal mouth with thickened lips and a lower jaw that is usually shorter than the upper. The slender outer teeth are very strongly recurved; anteriorly and anterolaterally in the lower jaw implanted procumbently; in the upper jaw nearly vertical or very slightly procumbent. The teeth of the inner series are small, predominantly unicuspid in fish of over 90 mm standard length and arranged in a broad band across the anterior part of each jaw, narrowing abruptly to a single row posterolaterally. There are 3-9 (rarely 2) rows in the upper jaw and 2-9 in the lower jaw (modal ranges 4-5, 3-4). The outer margin of the dentigerous surface of the lower jaw, over its anterior half, dips downwards and slightly outwards* (like described above for *Psammochromis*) *so that the insertions of the outer tooth row lie below those of the inner series. The range of the lower jaw length is 22-38% of the head length, the lower jaw is usually longer than broad.* I add to this definition that the lower jaw is usually between 1.1 and 1.6 times longer than broad.

A number of these characters are shared with the species of the *Psammochromis* lineage, from which *Ptyochromis* differs mainly by virtue of broad bands of inner teeth which are relatively small rather than tall, by more strongly recurved teeth in the outer rows, a broad lower jaw and a steep and often decurved dorsal head profile. From *Neochromis*, a lineage with similar head profile, *Ptyochromis* differs in dentition and in the anatomy of the lower jaw, from *Paralabidochromis* in dentition. From piscivorous haplochromines with unicuspid teeth, *Ptyochromis* differs by virtue of a broad and short lower jaw, as well as in tooth shape.

All described *Ptyochromis*, most of the undescribed species, and several oral shelling snail eaters of other lineages, share a dominant melanin pattern consisting either only of a prominent mid lateral stripe that can be interrupted, or of a prominent mid lateral stripe, superimposed by a less prominent "broken chessboard".

The described species of the *Ptyochromis* lineage live predominantly over sand bottoms. However, two, *H. (P.) sauvagei* and *H. (P.) xenognathus*, are frequently found in rocky habitats. Where these species are found at rocks, sand bottom is usually not far away, and is sometimes present in the form of small pockets among the rocks. During our rock shore survey we discovered several new species of oral shelling snail eaters that seem to be restricted to rocky habitats. Most of them are clearly assignable to the *Ptyochromis* lineage according to their anatomy. Thus, this largely sand dwelling lineage seems to have, at least at some places, been successful in establishing itself in the complex *Mbipi* communities.

Haplochromis (Ptyochromis) sauvagei (Pfeffer) 1896 is one of four described species of the *Ptyochromis* lineage. It is characterized by a steep dorsal head profile, and a dentition consisting of strong, recurved, in the lower jaw procumbent outer teeth. Greenwood (1957) described males as grey-green or blue-grey with a coppery sheen on the flanks and ventral aspects of the operculum. Populations that have the coppery sheen are known only from northern parts of Lake Victoria. Such populations, from Rusinga Island and the Migori River mouth, have several times been shipped from Kenya to Europe and the U.S. under the names *H. (P.)* "Rusinga sheller" and *H. (P.)* "Migori sheller" (Kaufman & Seehausen 1995). The populations in our survey area in the southern lake, however, have entirely light blue, males that can have but a little coppery flush on the chest. Interpopulation differences in male coloration within our survey area, are in *H. (P.) sauvagei* less apparent than among rock-restricted cichlids. However, recently we discovered (at Igombe Island) the first known population that has, apart from blue males, also yellow males (Seehausen & Bouton 1996b). Males of the blue morph in this population are particularly bright blue on the flanks and have an anal fin that is proximally pale blue-grey and only distally pale reddish. Males of the yellow morph, in contrast, have an entirely red anal fin. I cannot, currently rule out the possibility that we are dealing with a sibling species pair. Males

Haplochromis sauvagei; a male (above) and a female (below) from Kisumu.

of both forms have a blueish dorsal fin, and a proximally green-grey to blue-grey, distally red caudal fin. Females of all known populations are brassy yellowish, and have a bright yellow underside of the head. In some populations, however, entirely greyish females occur.

Many populations in our survey area have furthermore a piebald morph that is quite frequently found among females (black blotches on brassy-yellow ground) but rarely also among males (black blotches on whitish grey ground; Seehausen 1993). The melanin pattern of *H. (P.) sauvagei* consists of a simple mid lateral. Only frightened males can show six to seven vertical bars on the flanks. While the mid lateral stripe is continuous in the northern populations, it is in southern populations interrupted. Until the long shores between our survey area and Rusinga Island in Kenya have been sampled, it must remain an open

Haplochromis xenognathus; a male from Kissenda Island (above) and a female from Nansio Island.

question, whether the northern populations are conspecific with those from the South, and which of them is Pfeffer's *H. (P.) sauvagei*, if they are not conspecific. Northern populations have been treated as specifically distinct from *H. (P.) sauvagei* by Kaufman & Ochumba (1993).

H. (P.) sauvagei lives in habitats in which patches of sandy substrate are interspersed with patches of shelter. The shelter can be rocks, vegetation or both. It lives at water depths from less than 1 m to at least 5 m. This species is largely absent from pure rock habitats without pockets of sand. It feeds predominantly on snails. Small, soft-shelled snails can occasionally be crushed between the pharyngeal jaws. However, the usual feeding mode is oral shelling: The fish carefully approaches a moving snail and, when just a few millimetres are left that separate it from the prey, turns its head slightly sideways, waiting for a suitable moment to get with a sudden quick bite hold of the soft body of the snail. This is followed by jerking, to tear off the body or a part of it from the shell. Unlike in most real rock cichlids, in *H. (P.) sauvagei* both sexes are encountered in approximately equal frequencies. It frequently lives sym- and parapatrically with other oral shelling cichlids of the *Ptyochromis* lineage, mainly *H. (P.) xenognathus* and, at Igombe Island, also with *H. (P.)* "red rock sheller".

Haplochromis (Ptyochromis) xenognathus Greenwood 1957 seems closely related to *H. (P.) sauvagei* and represents, anatomically speaking, the more derived and specialized one of the two. Though this species is very variable in head shape, it has generally a less steep dorsal head profile than *H. (P.) sauvagei*, a longer, more pointed snout, and a more extreme version of the typical *Ptyochromis* dentition: The outer teeth are so strongly procumbent in the lower jaw that their necks lie almost horizontally and form an extension of the lower jaw of considerable length. At the same time they are that much recurved that the tip of each tooth points almost vertically upwards. Greenwood (1957) gives some drawings of this peculiar condition. The inner teeth are usually arranged in many (3-9) rows, forming a broad band anteriorly in each jaw. The lower jaw is anteriorly often that much decurved that the tips of the inner teeth, in lateral view, lie higher than those of the outer teeth. The lower jaw is often strongly retrognathous. However, in all characters concerning lower jaw shape and dentition there is considerable individual variation. It remains to be investigated, whether the different types represent more than one species. Male *H. (P.) xenognathus* are bright light blue to greenish grey. Blue males are usually caught over sand, while most males from rocky substrates are more greenish. Blue males usually have all fins blue, the soft dorsal fin, and the upper half of the caudal fin bear red streaks and maculae. Greenish males have more red in their fins, particularly in the anal fin, and they frequently have half red pelvic fins. Females are greyish, without the bright yellow colour of *H. (P.) sauvagei* females. From Greenwood's description, it is not quite evident which of the two male coloration types is the typical one for the species. It may well be that *H. (P.) xenognathus* from northern populations differ in coloration from the southern forms (Kaufman & Seehausen 1995).

While *H. (P.) xenognathus*, which is in our survey area widely distributed as an abundant sand-dweller, has at most rocky localities not or only exceptionally been caught, it is a frequent member of the rock cichlid community at a few places. Such a place is Igombe Island (southern Speke Gulf), where the blue sand-dwelling type intrudes into the sand-rock habitat interface from adjacent sand bottom. Two others are Kissenda Island (northwestern Mwanza Gulf) and Nansio Island (Ukerewe). The individuals caught there are bigger than those caught over sand. At Nansio Island our bottom sampler indicated soft substrates among the rocks and subsequent Scuba diving revealed a peculiar habitat situation. All horizontal rock surfaces were covered with organic sediment, grazed upon by uncountable snails. From 5 m water depth downwards, all pockets among the rocks were filled up by more than 10 cm thick layers of snail shells, among which sediment had accumulated. This unique situation, which may account for the very high population density of *H. (P.) xenognathus*, is probably due to the thick evergreen rainforest with high trees hanging over the water, that provide continuous litter supply. I observed large solitary males that, like other rock-dwellers, were hiding in gaps among the rocks.

The passibility that rock-dwelling populations of *H. (P.) xenognathus* differ from the typical sand-dwelling form remains to be investigated. A population that has longer lower jaws occurs at Zue Island (northern central Speke Gulf). It lives slightly offshore, over small boulder rock substrate, at depths beyond 3.5 m. The haplochromine community there is a real rock-cichlid one. Like those from the other rock-dwelling populations, males from Zue Island differ in coloration from the typical sand-dwelling *H. (P.) xenognathus.* Moreover, the outer teeth are not as procumbent, as in the typical *H. (P.) xenognathus*. The inner teeth are arranged in 4 to 5 rows and the pharyngeal teeth are somewhat enlarged. Like in *H. (P.) sauvagei*, and unlike in many other rock-dwelling cichlids, females and males of *H. (P.) xenognathus* are encountered over rocks in approximately equal frequencies. The species lives sympatrically with most other rock-dwelling *Ptyochromis*.

A typical *Ptyochromis* is the new ***Haplochromis (Ptyochromis)* "striped rock sheller"**. This very conspicuous species seems to be a real rock-dweller and is known only from geographically isolated rocky islands in the central Speke Gulf. Males grow large (table 3) and attain a stocky shape with a broad head and a steeply sloping dorsal head profile. Among the described species, *H. (P.) sauvagei* is closest to "striped rock sheller". The latter differs from *H. (P.) sauvagei* by a broader lower jaw, more blunt outer teeth and by coloration. Males carry a broad, deep black, and uninterrupted mid lateral stripe, traces of a dorsal lateral stripe and of three or four vertical bars on greyish ground that has often a faint flush of red on the dorsum. The dorsal fin is blue-grey with red lappets, the caudal fin proximally dark grey, distally red, the anal fin is red, and the pelvic fins are black. A peculiarity is that several of the big orange coloured egg dummies on the anal fin are confluent in about 75% of the males. The only other rock-dwelling haplochromine that we found with confluent egg dummies, is *H. (?)* "large eye pseudo-nigricans". The chest scales of *H. (P.)* "striped rock sheller" are usually small and deeply embedded.

H. (P.) "striped rock sheller" inhabits moderately steep and steeply sloping rock shores, with boulders of moderate and big size. Subadults can be found in very shallow water, but adults live at depths ranging from 2 to at least 5 m, but probably down to 15 m. The species is very rare. A big male from Vesi Islands had exclusively dark grey snail flesh in its stomach. Like in many other rock-dwelling cichlids, males of "striped rock sheller" are more frequently encountered than females.

Known from just one locality is ***Haplochromis (Ptyochromis)* "deep water rock sheller"**. It is the most deep bodied of the rock-dwelling *Ptyochromis* species, has a decurved, steep dorsal head profile, a very broad lower jaw, and a typical *Ptyochromis* dentition. The unicuspid teeth in the outer rows are rather stout, resembling the condition in *H. (P.) sauvagei* and *H. (P.)* "striped rock sheller". Those in the lower jaw are procumbent, those in the upper jaw are strongly recurved and also somewhat procumbent. The inner teeth are arranged in 4 to 5 rows in the upper, and 3 to 4 in the lower jaw. They are unicuspid and implanted so that they lie almost horizontally. The medial pharyngeal teeth can be enlarged but are not molariform. The chest scales are somewhat size reduced and deeper embedded, though not as much as in many other rock cichlids. *H. (P.)* "deep water rock sheller" differs from *H. (P.) sauvagei* by a broader lower jaw, from that species and from *H. (P.)* "striped rock sheller" in general appearance and coloration.

H. (P.) "deep water rock sheller" is a poly-

Haplochromis "striped rock sheller" from Ruti Island.

A male *H*. "deep water rock sheller" from Python Island.

morphic species. It has a blue and a yellow-red male colour morph just like the population of the snail crusher *H. (Labrochromis)* "stone" that occurs sympatrically with it (Seehausen & Bouton 1996). Males of the blue morph have entirely light blue flanks and, with these beautifully contrasting, blood red caudal and anal fins. The dorsal fin is blue-grey with red lappets, and the black pelvic fins can have some red in their soft parts. The other, less abundant morph has a red head and anterior dorsum, and greenish-yellow lower and posterior flanks. The anal fin is much less intensely coloured, but the dorsal fin is red. Females of "deepwater rock sheller" are more colourful than those of most other Lake Victoria haplochromines. Their flanks are greyish with yellow flush, their dorsal fin lappets and caudal fin margin light red, and their anal fin beautifully orange-red with orange-yellow spots in the position of male egg dummies. The melanin pattern is usually not prominent and consists of a mid lateral stripe and about five broad vertical bars.

H. (P.) "deep water rock sheller" seems to be a real rock cichlid. It is known only from an eight metre deep rocky trough between the two larger Python Islands, and is sometimes found elsewhere at these islands. Different from the aforementioned species, it is rather abundant in its habitat, or was abundant at least until 1993. In 1995 and 1996 we found it only in small numbers. It is not clear, why this species seems to be endemic to a place that is geographically poorly isolated. Python Islands are situated in the southern part of the central Mwanza Gulf, not more than 600 m from the mainland, and the surrounding waters are not deeper than 8 or 9 m. Very few species in that region are endemic to a single island. I assume that *H. (P.)* "deep water rock sheller" was in the pre-Nile perch time more widely distributed on rocky substrates in deep water, and that the population in the Python Islands trough is a relict population (Seehausen et al. in press [b]). The species may have gone extinct in most deep water rock-bottom habitats when the Nile perch invaded them. The narrow trough between the Python Islands may offer more protection against predation, than open rocky slopes do (see also under *H. (?)* "pseudoblue"). *H. (P.)*

Python Island as seen from the easternmost islet.

"deep water rock sheller" coexists there with other deep water dwelling rock cichlids like *H. (L.)* "stone", *H.* "pseudoblue" and *H.* "deepwater".

Of three individuals whose stomachs we examined, two had eaten predominantly snails, of which we found only the dark grey flesh. One of these two fishes had also a case of a Trichoptera larva in its stomach. The third individual had more diverse stomach contents, consisting to equal parts of snail flesh and zooplankton (!, *Daphnia*) and to a small part of chironomid larvae. We found neither shell fragments nor sand grains in the stomachs, confirming that the species is foraging on rock bottom (sand grains are commonly found in the stomachs of sand-dwelling *Ptyochromis*), and is shelling its snail prey. Some small pieces of wood were found in one stomach. Python Islands have dense evergreen vegetation of high bushes and small trees, many of which grow directly at the water level. Thus accumulation of dead wood at the ground of the trough between the islands is possible and may form a grazing substratum for snails (see also under *H. (P.) xenognathus*). *H. (P.)* "deep water rock sheller" lives in waters beyond 4 m, and down to at least 8 m depth. Like with many other rock cichlids we caught many males and very few females.

From "striped rock sheller" and "deep water rock sheller" quite different in head shape is ***Haplochromis (Ptyochromis)* "Zue sheller"**. The species, which is known only from Zue Island, is shallow bodied with a dorsal head profile that is usually less steep than that of the other two species. Among the known rock-dwelling *Ptyochromis*, this one has the least broad lower jaw (table 3). Although it is narrow, the lower jaw is in other respects typically *Ptyochromis*: retrognathous, dipping anteriorly downwards, and its outer teeth are procumbent. The dentition of "Zue sheller" somewhat deviates from the typical *Ptyochromis* condition. The outer teeth are weakly bicuspid to unicuspid, and only slightly recurved. The inner teeth are arranged in only 2 to 3 rows. Males are blueish grey on the flanks with a dark, uninterrupted mid lateral stripe. Their dorsal fin is dark grey with red lappets, the upper half of the caudal fin grey with a red margin, the lower half entirely red, the anal fin is wine red with large orange-yellow egg dummies. The pectoral fins are black. Females have not yet been found. *H. (P.)* "Zue sheller" lives sympatrically with *H. (P.) xenognathus* on the gently sloping island shelf with small rock boulders. While the latter species is found from shallow to deeper waters, *H. (P.)* "Zue sheller" is restricted to depths beyond 3 m and is quite rare. Two individuals, the stomachs and intestines of which we examined, had eaten exclusively soft parts of snails.

While the above discussed three new species of rock-restricted *Ptyochromis* live predominantly in deeper waters, two other new species are found in shallow waters. Different from the other rock-dwelling *Ptyochromis*, they have a red male coloration. ***Haplochromis (Ptyochromis)* "red giant sheller"** must be very rare and is known from only two male individuals. One was collected at Kissenda Island in the northwestern Mwanza Gulf, the other one about 8 km further north at Irondo Point, immediately west of the entrance to the gulf. Both were bright red on the flanks, most intensively so behind the pectoral fins. All unpaired fins were bright red, only the spinous parts of dorsal fin and pelvic fins were dark. "Red giant sheller" may deviate from other species of the *Ptyochromis* lineage in its melanin pattern. The two males showed 6 to 7 vertical bars on the flanks but no mid lateral stripe. However, more individuals have to be seen to know whether this is consistent.

H. (P.) "red giant sheller" is one of the largest oral shellers. Its dorsal head profile is decurved and slopes steeply. Its outer teeth are less strong than in the before discussed steep headed species, and are moderately to strongly recurved. The inner teeth in the upper jaw form a broad band, as is characteristic for the lineage. However, in the lower jaw, this band is in one of the individuals less broad. Even a large male has many weakly tricuspid teeth in the inner tooth rows, while individuals of the before discussed species of comparable size have usually only unicuspid inner teeth. Thus there are some indications that *H. (P.)* "red giant sheller" is anatomically less specialized a snail sheller than most other *Ptyochromis* species.

At both localities this species lives at moderately steep rock shores with medium sized boulders and must be very rare at least at Kissenda Island (Irondo Point has only once been sampled). We caught both males at water depths of between 1 and 2 m. At both places they lived in sympatry with *H. (P.) xenognathus*, at Kissenda Island furthermore with the snail crusher *H. (Labrochromis)* "stone", and at Irondo Point with *H. (Psammochromis)* "red zebra" that may be another little specialized snail sheller. From the latter species which has similar male coloration, *H. (P.)* "red giant sheller" differs in head profile, head and jaw width and dentition. From the second red *Ptyochromis* like rock-dwelling species, *H. (P.?)* "red rock sheller", it differs in size, head shape and dentition (table 3). Also from other entirely red rock cichlids, it is distinguished by its head shape and oral dentition. *H. (Xystichromis)* "red carp", that lives in sympatry with *H. (P.)* "red giant sheller" at Kissenda Island, has scraper dentition. *H.* "red pseudonigricans" has a shallower dorsal head profile, much narrower jaws, much finer, bicuspid and not recurved outer teeth, and fewer inner tooth rows. With its coloration and deep body, *H. (P.)* "red giant sheller" resembles some pharyngeal crushing snail eaters from sublittoral mud bottoms (*H. (Labrochromis) teegelari*, *H. (Labrochromis) mylergates*). These species have strongly enlarged molariform pharyngeal teeth. In contrast, *H. (P.)* "red giant sheller" has only fine and slender teeth on the pharyngeal bones.

The second shallow water dwelling species with red males and an oral sheller-like dentition deviates even stronger from *Ptyochromis* as defined by Greenwood. The outer teeth of ***Haplochromis (?)* "red rock sheller"** are slender bicuspids. Those in the lower jaw, which is hardly anteriorly decurved, are procumbent, those in the upper jaw slightly to moderately recurved. The inner teeth are arranged in just two rows in both jaws, are tricuspid and slightly recurved. *H. (?.)* "red rock sheller" is a rather elongated species with a decurved but not steep dorsal head profile. Its chest scales are small and deeply embedded like in the majority of the rock-dwelling haplochromines. Clearly is this species anatomically less specialized for snail shelling than all aforementioned *Ptyochromis* species. It is the slenderness, recurvature, and procumbent implantation of the outer teeth, together with the relatively steep dorsal head profile that suggest at least an anatomical relation of this small species to *Ptyochromis*. However, it may phylogenetically as well be closer related to some small sand-dwelling insectivores.

Males are blueish with bright red gill covers, chest and anterior flank. Further caudad the flanks become yellowish. The underside is dark grey-green, the dorsum grey. The dorsal fin is bright blue with red streaks in the soft part, caudal and anal fins are proximally blue and distally red, the anal fin with mostly two big orange coloured egg dummies. Females are light whitish yellow. The melanin pattern deviates from the typical *Ptyochromis* pattern, because the mid lateral stripe is very faint while vertical bars are frequently seen. The light coloration of females is typical for sand-dwelling, rather than for rock-dwelling cichlids. The male is rather dark, but its egg dummies are much bigger than in other rock cichlids from shallow waters. However, we never found this species over real sand bottoms. Rather it seems to be replaced over sand by the similar *H. (?)* "bright red sheller" (Seehausen 1993).

We know *H. (?)* "red rock sheller" from just three places, Igombe Island, Mponze Point, and Bwiru Point at the southern Speke Gulf coast. The habitat at Igombe Island is a moderately steeply sloping rock shore, composed of small to medium sized boulders. Here it is by far the most abundant species in shallow waters, and lives as a real rock cichlid, though

A male *H*. "Zue sheller" from Zue island.

A male *H.* "red giant sheller" from the northwestern part of the Mwanza Gulf.

A male *H*. "red rock sheller" from Igombe Island.

large plains of open sand bottom are surrounding the rocky reef. Males occupy territories among the rocks from the surface to about 3 m depth, far away from the sand-rock interface. These territorial males are brightly coloured and very active, courting females that are passing by, in much the same manner as other rock cichlids do. They are quite aggressive, and frequently chase other rock cichlids away from their territories. Females move in shoals, usually mixed with other species such as *H. (P.) xenognathus*, *H. (P.) sauvagei*, and female *H. (Xystichromis)* "copper black" and *H. (Neochromis)* "velvet black". These shoals struggle in the currents of the strong surf in shallow water, and are often seen over big flat rocks, from which they pick up food items. Shoals of female haplochromines are also seen at greater depths, but already at 2.5 m depth, *H. (?)* "red rock sheller" is lacking among them. At Mponze Point "red rock sheller" lives in a very gently sloping rock-sand mixed habitat in very shallow water. Its habitat at Bwiru Point is characterized by very big, steeply sloping boulders, but the species is rare there.

High abundances of oral shellers in shallow waters are characteristic for sandy substrates while we did not find them over purely rocky substrates, except in the peculiar situation at Nansio Island (see under *H. (P.) xenognathus*) and at Igombe Island. The high abundance of *H. (?)* "red rock sheller" in shallow water at Igombe Island is not quite explained. It may have to do with the proximity of large sandy plains. The stomach of a male from Igombe contained unidentifiable smashed material and lots of sand, its intestine contained to about equal parts ostracods and may fly larvae, as well as a few chironomid larvae. The presence of much sand in the stomach indicates that the fish has been foraging over sand. Possibly *H. (?)* "red rock sheller", though reproducing among the rocks, partly utilizes the sand bottom that borders the rocks at 4-7m depth, as foraging ground.

A mill in the throat — snail crushing haplochromines

Apart from some above described species of the *Psammochromis* lineage that have enlarged teeth on the pharyngeal jaws, there are currently about 13 species of anatomically specialized pharyngeal crushing snail eaters known from Lake Victoria (Witte & van Oijen 1990, Witte et al. 1992, Kaufman & Ochumba 1993, Seehausen et al. in press [b]), seven of which are described (Greenwood 1980). Unlike some *Psammochromis* that crush predominantly bivalves and ostracods, most of these species crush also hard snail shells like those of *Melanoides tuberculata*. One, *Astatoreochromis alluaudi* is not a member of the Lake Victoria species flock, and not endemic to the lake (see page 255ff). Four of the five other described, and several undescribed species inhabited sublittoral soft bottoms, and disappeared in the course of the Nile perch upsurge (Witte et al. 1992). One described species (*H. (Labrochromis) pharyngomylus*) was living over sand before the Nile perch came up, and three undescribed species in our survey area inhabit rocks. We never found more than one species at any one locality. Interestingly their distribution and that of bivalve crushing *Psammochromis* and similar species (*H. (P.)* "striped crusher", *H. (P.) riponianus*, *H. (?)* "yellow giant") is also largely exclusive. However, species of both groups usually live sympatrically with the snail crusher *Astatoreochromis alluaudi*. In most such cases *A. alluaudi* lives in shallower waters than the other species.

Greenwood (1980) considered the pharyngeal crushing snail eaters of Lake Victoria with a strongly hypertrophic pharyngeal mill (except *Astatoreochromis alluaudi*) a monophyletic group, and gave them generic status, resurrecting the genus *Labrochromis* Regan 1920. He defined this lineage as *haplochromines characterized by a massive hypertrophy of the pharyngeal mill, pharyngeal dentition that* *is composed almost entirely of stout molariform teeth, and stout but generalized oral jaw teeth. The outer jaw teeth are of the basic bicuspid type in small individuals and even in fishes bigger than 100 mm standard length, an exclusively unicuspid dentition is uncommon. The teeth are moderately stout to stout with a subcylindrical neck and the crown is not markedly compressed. The teeth forming the inner series are small, tricuspid, and are arranged in 1-3 (rarely 4) rows anteriorly and anterolaterally in both jaws. The fishes have a typically generalized facies, but most species have a "heavy headed" appearance. Their mouth is horizontal or very slightly oblique, the jaws are isognathous, the premaxilla* (tooth carrying upper jaw bone) *is not produced into a beak or shelf, the lips are not thickened. The dentary* (tooth carrying lower jaw bone) *is slender and shallow, the lower jaw length ranges from 34-44% of the head length (modal range 37-40%).*

The only derived character in this definition, which serves to distinguish the lineage from other lineages with a generalized facies, is the degree of hypertrophy of the pharyngeal mill. This may not be a very strong argument for a monophyletic origin of the lineage. However, as I discussed in the chapter on taxonomy, I do not think the arguments that have been brought forward against Greenwood's phylogenetic hypothesis, provide unambiguous evidence.

The rock-dwelling pharyngeal crushers have strongly enlarged pharyngeal bones with broad molariform pharyngeal teeth, the so called pharyngeal mill. Their oral teeth are usually blunt unicuspids in the outer row and the inner teeth are arranged in not more than 2-2.5 rows. However, apart from this, they have little in common and they may well be derived from more than one phylogenetic lineage. Only one species exhibits all characters that Greenwood used in the definition of the genus *Labrochromis*. Another one is in some characters closer to *Psammochromis*, and the third one to *Paralabidochromis*.

***Haplochromis (Labrochromis)* "stone"** is the largest known snail eater, reaching about 150 mm standard length. Its distribution is a typical central/northern Mwanza Gulf one, similar to that of some species of the Vertical bar *Mbipi*. We know it from almost all sampled stations between Python Islands in the south, Bwiru Point in the northeast, and Amranda Point in the northwest. It is absent from the southern Mwanza Gulf south of Python Islands and is replaced by other pharyngeal crushing species (mostly of the *Psammochromis* lineage) in the Speke Gulf.

Male *H. (L.)* "stone" occur in two basically different colour morphs (Seehausen & Bouton 1996). One is blue on the entire body, including the dorsal fin, usually with many red maculae in the soft part of the latter. The caudal fin is blue-grey with red streaks and maculae, or largely red, the anal fin is proximally blue-grey, distally faint red or almost entirely red, with yellow egg dummies. The other morph is bright red on the dorsal head surface, gill cover, anterior flanks, and anterior dorsum, and yellowish on the remaining flanks. The fin coloration resembles that of the blue morph, but the red colour in the dorsal fin can extend into the spinous part. Females are yellowish brown with 4 or 5 broad vertical bars on the flanks. Adults can easily be identified by their massive head, and the strongly enlarged pharyngeal teeth that can be seen even with the naked eye on the living fish, if the latter is large enough. One just needs to hold such a fish head-up, and look into its throat. However, if the fish is not very large, an otoscope will be needed for magnification. Juveniles and subadults somewhat resemble fishes of the *H.* "pseudonigricans" complex. However, the red spots in the soft part of the dorsal fin, that are usually prominent also in small individuals, often allow to identify *H.* "stone" even before the pharyngeal teeth are noticeably enlarged. At Python and at Kissenda Islands we collected a few big blue males whose pharyngeal bones were only slightly enlarged, and whose pharyngeal teeth were not molariform but just a bit coarser than generalized teeth. These individuals either represent a separate species or are a second, most likely insectivorous trophic morph of *H. (L.)* "stone". They live sympatrically with blue and red males with hypertrophied pharyngeal mill.

At most places where we found *H. (L.)* "stone", moderately steep to steep slopes, with medium sized to very large rock boulders, dominate the habitat. Subadult individuals are frequently caught in shallow inshore waters between rock boulders. Adults inhabit greater depths. At the moderately steep Python Islands they live somewhat offshore at depths ranging from 3 to at least 8 m. At very steeply sloping places, e.g. Anchor Island and Nyegezi rocks they are found inshore and from 1.5 m depth downwards. At such places the habitat overlap with the shallow water dwelling snail crusher *Astatoreochromis alluaudi* is largest. *H. (L.)* "stone" is at some places rather abundant, for instance in the deep trough between the Python Islands, where it lives in sympatry with another big snail eater, the snail shelling *H. (Ptyochromis)* "deepwater sheller". The diet of *H. (L.)* "stone" consists predominantly of snails but insect larvae are eaten as well (Bouton et al. submitted). *H. (L.)* "stone" seems to be one of the most mobile rock-dwelling cichlids (Seehausen et al. in press [b]), and is one of the few species that can sometimes be encountered over sand, several metres away from rocks.

While *H. (L.)* "stone" lives in sympatry with oral shelling molluscivores and the crusher *Astatoreochromis alluaudi*, we found it only at Hippo Island sympatrically with another pharyngeal crushing molluscivore. At Hippo Island, *H. (L.)* "stone" lives predominantly in crevices among inshore rocks, while *H. (P.)* "striped crusher" occurs slightly offshore but is very rare. Before the Nile perch upsurge *H. (L.)* "stone" must have been in parapatric contact with several mud bottom and sand bottom dwelling species of the *Labrochromis* lineage. One of these is *H. (L.)* "purple miller" (Witte et al. 1992) which is in coloration very similar to the red morph of *H. (L.)* "stone". The latter differs from the mud bottom dwelling "purple miller" by virtue of smaller egg dummies and outer teeth that are upright, rather than recurved as in "purple miller".

At Zue Island near Nafuba in the northern Speke Gulf lives a quite different pharyngeal crusher. This species, ***Haplochromis (?)*** **"Zue crusher"**, differs from *H. (L.)* "stone" in head shape and coloration and from *H. (Psammochromis)* "striped crusher" in oral and pharyngeal dentition, and in male coloration. Its dorsal head profile is less steep than that of *H. (L.)* "stone", the head is less broad and appears less heavy. The teeth in the outer tooth row on the oral jaws are short, stout, and blunt unicuspids of the *Labrochromis* type. They are very slightly recurved and slightly procumbent in the lower jaw, somewhat reminiscent of the condition in *Psammochromis*. The teeth in the inner rows are unicuspid. Males are wine reddish on the gill covers and anterior flanks, greenish on the remaining flanks. The greyish dorsal fin has many wine red maculae in its soft part.

I can currently not assign *H. (?)* "Zue crusher" to any of the described lineages. It might be a member of the *Labrochromis* lineage but may alternatively be an extreme crusher type of the *Psammochromis* lineage to which it shows some resemblance as well. It lives at the gently sloping small boulder shore of Zue Island offshore at depths beyond 4 m and is very rare. Once more individuals have been found, its relationships may become more clear.

Haplochromis (?) **"Sozihe crusher"** is the second rock-dwelling pharyngeal crusher that I cannot currently assign to any lineage. Known as yet only in one individual from Sozihe Islands, the eastern most of our sampling places, this species may be more widely distributed east of the surveyed area. From both foregoing species it differs in coloration and dentition. The male is on the flanks blue with purplish sheen, and carries a melanin pattern reminiscent of a chessboard pattern, though the vertical bars are but faintly visible. The grey-blue dorsal fin has red lappets, the caudal fin is largely red and the anal fin orange-red anteriorly and distally and grey-blue near the basis, where some small dark yellowish egg dummies are positioned.

A male *H*. "stone" from Anchor Island.

A female *H*. "stone" from Kilimo Island.

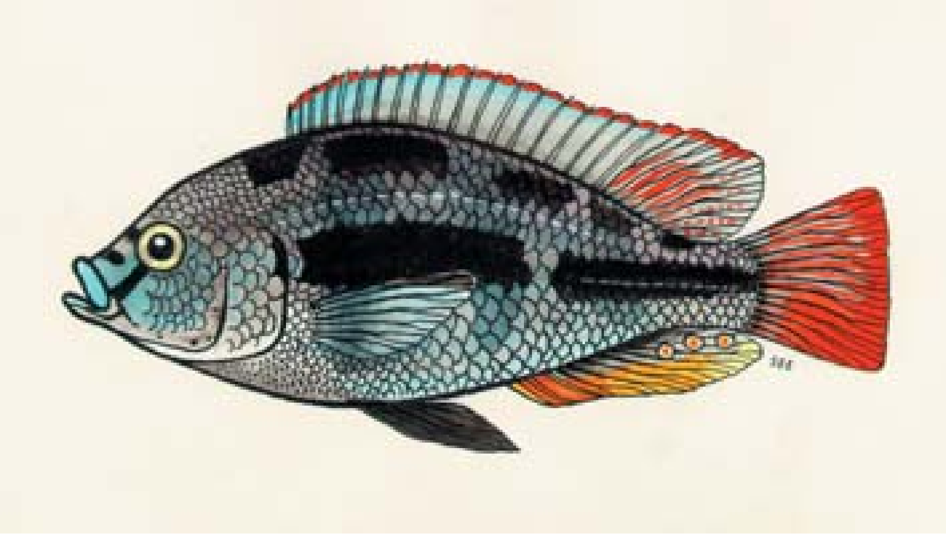
A preserved *H.* "Zue crusher" from Zue Island.

The rocky shore of Python Island.

The teeth in the outer row of the 103 mm (SL) long fish are blunt and stout weakly bicuspids and unicuspids, that are procumbent in the lower jaw. The inner teeth are weakly tricuspid and stand upright. The shape and arrangement of the teeth is somewhat reminiscent of that in some species of the *Paralabidochromis* lineage (e.g. *H. (P.) crassilabris*). So is the slightly thickened upper lip and the melanin pattern. However, the pharyngeal teeth are molariform, but Kaufman and Ochumba (1993) reported molariform pharyngeal teeth in a member of the *Paralabidochromis* lineage (*H. (P.)* "rockkribensis", page 162). More fishes of this interesting snail crusher need to be collected before more about its taxonomical position can be said. We caught "Sozihe crusher" at a moderately steep rock shore with rather big boulders, together with *Astatoreochromis alluaudi*, but no other pharyngeal crushing haplochromines. The water depth was about 6 m. The male had eaten predominantly planorbid snails of about 2 mm shell diameter. They made up 90% of the complete intestine contents. The remaining 10% were made up by chironomid larvae.

Mgobegobe — fish eating haplochromines of rocky shores

The ecological group of fish eating haplochromines can be subdivided into predators of free-swimming fishes (piscivores *sensu stricto*), species that prey upon eggs and buccal-stage larvae in the mouth of brooding females (paedophages) and those that steal the eggs of spawning pairs (egg-snatchers) (Greenwood, 1974, Witte & van Oijen 1990). Fish eaters *sensu stricto* are characterized by relatively large heads and long jaws (the lower jaw length is usually greater than 45% of the head length), armed with slender, recurved and acutely pointed unicuspid teeth, suitable to grasp their mobile prey. They are known at the southern lake shore as "*Mgobegobe*", and form the most species rich ecological group among the known Lake Victoria haplochromines. More than 130 species are known (M. van Oijen pers. comm.), of which 49 are described. Though with the discovery of the large group of *Mbipi* it has become clear that the proportion of piscivores in the Victorian flock was overestimated in the past (Greenwood 1974, Goldschmidt & Witte 1992), their extraordinary diversity is an



A male *H*. "Sozihe crusher" from Sozihe island. Drawing by Helmut Seehausen.

outstanding character of the Victorian cichlid species flock (Seehausen 1996). Ecological and taxonomical diversity of piscivorous Lake Victoria haplochromines are dealt with in some detail in a number of publications (Greenwood 1962, 1974, 1980, Fryer & Iles 1972, van Oijen 1982, 1991).

Regrettably a very large part of this predator diversity has been recently lost. Concomitantly with the population boom of the top predator Nile perch, populations of piscivorous haplochromines crumbled, and most of the species are currently considered extinct (Witte et al. 1992). During the past five years we found less than ten species of piscivores in southeastern Lake Victoria, most of them at rocky shores. Some of these have always been stenotopic rock-restricted species, others lived in a wider range of habitats before the Nile perch boom, but survived only in rocky habitats. In such cases it is quite unclear how sustainable in the long run the refugial populations are. Most piscivores naturally occur in low densities (van Oijen 1992), and many of their current rocky refugia are rather small rocky reefs and islands, that may accommodate only a relatively small number of individuals of big predators. If gene flow between these island populations is limited or entirely cut off by Nile perch predation, the long term viability of populations is hard to predict. Another effect would be that the now isolated remnants of originally panmictic populations (with random mate exchange over larger distances), will go their own way in their further evolution.

Greenwood divided the majority of the fish eating Lake Victoria haplochromines into two lineages, which he allotted generic rank in his last revision: *Harpagochromis* Greenwood 1980, and *Prognathochromis* Greenwood 1980. *Harpagochromis* is defined as *large growing haplochromines (146-200 mm standard length) with a body depth between 30 and 42% of the standard length (modal range 34-36%) and a long lower jaw (43-61% of the head length on species average). The anterior and anterolateral regions of the premaxilla are not produced to form a distinct beak or peak. The outer jaw teeth are strong and recurved; they are unequally bicuspid and unicuspid in fishes of less than 90 mm standard length but exclusively unicuspid in fishes over 120 mm standard length. The inner teeth are arranged in 1 or 2 (rarely up to 5) rows in each jaw.*

Prognathochromis is defined as *mostly large growing haplochromines (70-230 mm standard length) with a body depth between 24 and 45% of the standard length (mostly 30-34%) and a long lower jaw (41-62% of the head length on species average). The premaxilla are anteriorly distinctly beaked or peaked. The outer teeth are strong and recurved; they are mostly unicuspid in fishes of more than 90 mm standard length, and unequally bicuspid and unicuspid in smaller fishes. In one complex of species, tricuspid teeth are laterally and anterolaterally interspersed amongst the unicuspids. The inner teeth are arranged in 2 or 3 (rarely 1 or up to 6) rows in each jaw.*

Furthermore important are a number of qualitative and quantitative characters of the skull (neurocranium) that, according to Greenwood, serve to separate the two genera (see for details Greenwood 1980, van Oijen 1991). Van Oijen (1991) found that they seem to form continuous morphoclines in which any division would be arbitrary, and thus, considered a splitting of the piscivores into two genera not desirable. As I discussed in the chapter on taxonomy, I agree with him that some species may have been assigned by Greenwood (1980) to the wrong genus, but I think the data are not suitable to reject Greenwood's subdivision of the piscivorous Lake Victoria haplochromines into two major lineages. Therefore I keep here to Greenwood's classification.

Regrettably very little is known about hunting behaviour of Lake Victoria piscivores. This is so because the relatively murky waters of Lake Victoria make underwater observation of fast moving predatory fishes almost impossible. Greenwood did some feeding experiments with *Haplochro-*

mis (Prognathochromis) gowersi in an aquarium. He wrote the following about it. "For some minutes after the prey was introduced, the predator remained stationary or slowly aligned itself with the prey. Then it suddenly darted forward, inevitably catching the prey fish by the caudal peduncle. Never once did I see a frontal attack. The prey struggled for a short while but soon became motionless. The predator appeared to make no further attempt to swallow its food, although slight, almost trembling jaw and opercular movements were detectable (apparently to macerate the prey; my words). After four or five minutes the prey fish was released. The greater part of its caudal musculature had been grated away... The predator then either took hold of its prey from behind, and continued to rasp away the caudal region, or it positioned itself for a frontal attack. The latter course resulted in the head and forepart of the prey being taken into the mouth. This, of course distorted the predator's mouth and branchial region and it gulped and 'chewed' vigorously for some eight to ten minutes. At the end of that time only the prey's caudal fin protruded from the jaws. In all, the process of capture and ingestion took from fifteen to twenty minutes" (Greenwood 1962). Thus *H. (P.) gowersi* and probably many other Lake Victoria piscivores cannot swallow their fish prey as a whole, but rather have to macerate it piece by piece between their fine and sharp pharyngeal teeth (see also van Oijen 1989).

We currently know five species of piscivorous haplochromines that are still found at rocky shores. More species used to be found over rocks but disappeared during the last decade. Two ecological groups can be distinguished among them. The species of one group inhabit the rock surface, and are never found in crevices between the rocks (at least four species of "rock surface hunters"). Those of the other group live in caves, crevices and gaps among the rocks, and are never found outside of such (two known species of "rock crevice hunters"). All rock-dwelling species belong to Greenwood's *Harpagochromis* lineage.

Haplochromis (Harpagochromis) guiarti (Pellegrin) 1904 was in the "pre-Nile perch era" the piscivore most frequently encountered at rocky shores (F. Witte & M. van Oijen pers. comm.) in the Mwanza Gulf. It has from that area entirely disappeared in the course of the 1980s. Unlike some other rock-dwelling cichlids that went extinct in the Mwanza Gulf, we could not find *H. (H.) guiarti*, or similar species anywhere else either, nor has it been seen in northern parts of the lake (Kaufman & Ochumba 1993). It used to be restricted to sand, shingle and rock substrates but was geographically widely distributed in the lake (Greenwood 1962). According to Greenwood, males are dorsally malachite green, shading to silver ventrally. All fins are colourless except the black pelvics and the dark caudal fin. The three to four egg dummies are bright orange. Females are similarly coloured but have light yellow pelvics and but small orange spots in place of the egg dummies. *H. (H.) guiarti* is an, anatomically speaking, relatively little specialized piscivore, whose body and head shape is close to that of large "*Astatotilapia*"-like insect eaters (e.g. "*A*". *brownae*), and whose inner teeth usually retain the tricuspid condition found also in various insect eaters. It feeds predominantly upon juvenile cichlids but also upon large insect larvae and plant tissue (Greenwood 1962).

Haplochromis (Harpagochromis) serranus (Pfeffer) 1896 was one of the first Lake Victoria cichlids to be described. It is a large growing species, but in terms of head anatomy also relatively little specialized, compared to many other fish eaters (Greenwood 1962). Greenwood recorded it from several places in Uganda, two in Kenya and one in Tanzania. We found at two rocky islands in the Speke Gulf large growing fish eaters that probably belong to this species. They agree with Greenwood's redescription of the types in general appearance, coloration, melanin pattern and dentition. A characteristic feature of the latter is that the lateral ones of the unicuspid outer teeth are

A female *H. cf serranus* from Zue island.

A male *H. guiarti* from the Mwanza Gulf, collected and photgraphed in 1978.

more strongly recurved than the anterior ones. However, our rock-dwelling fishes are slightly more slender than the fishes Greenwood described.

Reproductively active males have a brownish grey dorsum and head, a white lower lip, and are metallic greenish to blueish on flanks and caudal peduncle. The dorsal fin is grey-blue with red lappets, the caudal grey with red margin and also the anal fin is proximally grey and only distally reddish. It carries a few orange or orange-yellow egg dummies. Van Oijen (in Greenwood & Barel 1978) published a very similar description of male coloration of *H. (H.) serranus.* Females of the rock-dwellers are light yellowish brown, tending to silvery on the under-

A male *H*. "big blue hunter" from Vesi Island.

A female *H. cavifrons* from Vesi Island.

sides, and exhibit a distinct dark mid lateral stripe and a dorsal lateral stripe that is usually also distinct. The fins are transparent. On the yellowish anal fin are usually some distinct yellow-orange spots in the position of male egg dummies. If quiescent, also males exhibit distinct mid lateral and dorsal lateral stripes. Particularly when seen under water *H. (H.) serranus* is easily recognized by its melanin pattern.

H. (H.) serranus differs from the similar *H. (H.)* "big blue hunter" in having a more strongly prognathous lower jaw, more strongly thickened lips, more bullate maxillae, that are only partly covered by the preorbital bone, and fewer tooth rows. As its major habitat Greenwood (1962) mentioned shallow waters with mud, though he found the species also over sand and shingle. We know the species from two localities in our survey area, the gently sloping small rock boulder habitat of Zue Island in the northern Speke Gulf, and the gently sloping rock habitat with medium sized boulders of Makobe Island in the southwestern Speke Gulf. The current disjunct distribution of *H. (H.) serranus* in our survey area is almost certainly a consequence of the Nile perch upsurge. At Makobe Island the population density of this predator is very low and it is observed only in somewhat deeper waters between 3 and 6 m depth. At Zue Island its density is higher, or was so until a few years ago, and the species lives at depths ranging from less than one metre to at least 5 m. A 20 cm (SL) long male from Makobe Island whose stomach contents we inspected, had swallowed a juvenile haplochromine. The length of the prey fish, recalculated from the length of its pectoral fins, was about 22 mm standard length. At a time when many females of algae scrapers guarded their fry in shallow water at Zue Island, I observed *H. (H.) serranus* roaming around in those shallows within shoals of non-brooding algae scrapers. In this way it may approach its prey, juvenile and subadult cichlids, unrecognized.

H. (H.) serranus seems to be one of the few larger piscivorous haplochromines, that survived the Nile perch boom at a number of places. I found it in 1989 also at rocks near Jinja/Uganda, and it has more recently (1992) again been recorded from there by A. Meyer (pers. obs.), and elsewhere in northern Lake Victoria by Kaufman and Ochumba (1993). Unfortunately nothing is known about population structure and gene flow between the refugial populations. For successful conservation it is desirable to know whether the currently surviving populations are isolated from each other or not, and whether the rock-dwelling populations are distinct from those that live or lived over soft bottoms. The chest scales of *H. (H.) serranus* from the two rocky islands in our research area are somewhat size reduced and deeper embedded, compared to the generalized condition found in most non-rock-dwelling cichlids.

***Haplochromis (Harpagochromis)* "big blue hunter"** is another big piscivore that probably belongs into the closer phylogenetic neighbourhood of *H. (H.) serranus*. It differs from the latter by a slightly convex rather than straight dorsal head profile; a shorter, broader and not prognathous lower jaw; maxillae that are completely hidden under the preorbitalia when the mouth is closed; finer outer teeth, that are less recurved, and are laterally not more recurved than anteriorly; more inner tooth rows; and by male coloration. Males are light blue on the flanks, shading to blue-grey dorsally and on the head. The dorsal fin is blue-grey with red lappets like in *H. (H.) serranus*, but the red in the caudal fin is more extensive and the anal fin is entirely pale red with rather small orange-yellow egg dummies. Until now we collected only males in breeding dress. These did not exhibit a mid lateral stripe. However, females and non breeding males may exhibit it.

H. (H.) "big blue hunter" is known only from the Vesi Archipelago in the central Speke Gulf. It inhabits a moderately steeply sloping shore, with medium sized rock boulders, which is part of a broad rocky shelf, lying between the shore and at least 10 m water depth. We found large sexually active males at depths of around 4 to 5 m, but it is likely that the species uses the entire rocky shelf as its hunting ground. I consider this species critically endangered.

Haplochromis (Harpagochromis) cavifrons (Hilgendorf) 1888 is, like *H. (H.) serranus*, one of the first cichlid species that were described from Lake Victoria. It must have been widely distributed before the Nile perch boom, and had been recorded from various places (Greenwood 1962). After the Nile perch boom it had not been seen for many years. Recently we caught one female on the very rocky shelf in the Vesi Archipelago, on which also *H. (H.)* "big blue hunter" survived. *H. (H.) cavifrons* has a unique melanin pattern, consisting of irregular dots and blotches, distributed over the entire body and head, and giving the fish a freckled appearance that is not known from any other Lake Victoria cichlid. According to Greenwood (1962) males have an olive to yellow-brown ground colour, shading to silvery below, and a dark brown head. Dorsal and caudal fins are yellowish, sometimes with traces of deep red. The anal fin is proximally dark, reddish to pinkish distally, and with yellow egg dummies. The pelvic fins are black and pink. Females have similar coloration, except that pelvic and caudal fins are yellow. Our female does not have dark blotches on these fins, as described by Greenwood. Greenwood mentioned that his females from the Mwanza area were dark olive green instead of yellow-brown. Our individual from the Speke Gulf is of the yellow-brown colour type.

In contrast to the two above discussed species, *H. (H.) cavifrons* has the outer teeth only slightly recurved. The individual from Vesi Islands agrees in this respect with the fishes Greenwood used for his re-description of the species, but it has a shorter lower jaw and narrower interorbital width than the latter. *H. (H.) cavifrons* seems to predominantly inhabit hard bottoms. From its rarity in beach seine catches, and regular presence in offshore set gill-nets, Greenwood postulated that it might not be a member of the inshore community. Alternatively, pure sand habitats, that fishermen usually select for beach seining, may not be its preferred habitat. Gill-nets can also be set over rocky or mixed bottoms. We caught our fish on the rocky shelf in 4-5 m deep water.

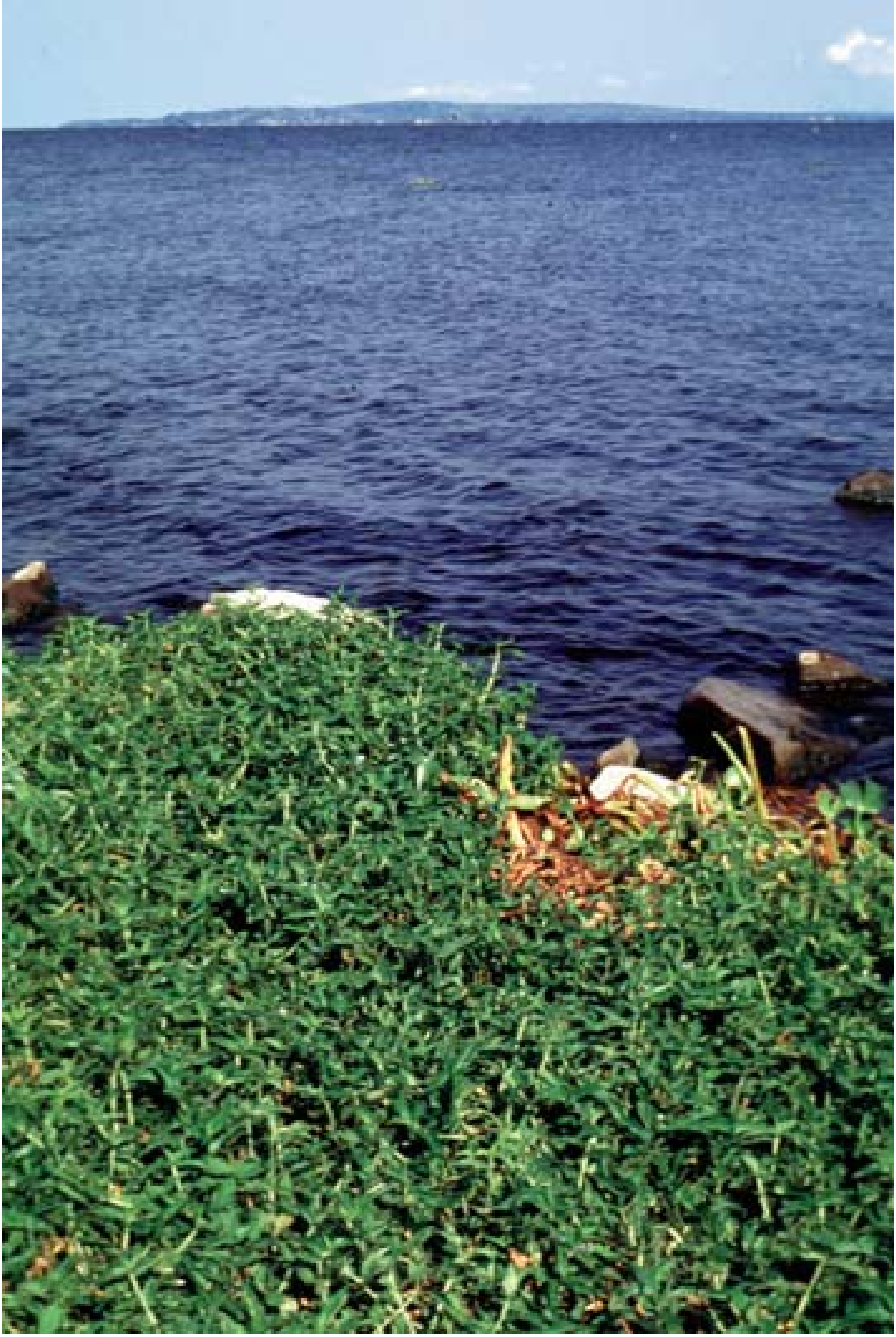
Haplochromis (Harpagochromis) howesi van Oijen 1992 is the only described species of rock crevice hunters. Strictly speaking it is, according to van Oijen (1992), not a piscivore but a crab eater (see below). From all but one (otherwise very different) described piscivores of Lake Victoria *H. (H.) howesi* differs by having small scales between some spines and rays of dorsal and anal fin. These scales are usually arranged in short rows of two to five, sometimes more scales, rising from the fin basis. Sometimes a single scale can exist between the rays, isolated from the fin basis. The fin scales can be very difficult to find since they can be embedded under a pigmented epithelium.

Males of *H. (H.) howesi* are very dark brown-black, with a flush of dark orange over the pectoral fins. The dorsal fin is dark grey with blackish lappets, the caudal fin brown-black, sometimes with a faint pinkish flush. The anal fin is dark red in its anterior two thirds and brownish posteriorly. The egg dummies are orange-yellow to dark orange. The pelvic fins are black, with frequently some reddish flush in the soft part. Van Oijen described females as dorsally dark brown-grey, ventrally on the flanks greenish, and having greenish yellow fins. The individuals used for the description were all from places in the northern Mwanza Gulf. We caught two big females in the Speke Gulf that had dark grey fins. One of them, as well as all unidentified subadults of the *howesi* group (see below) that we collected in the northern Mwanza Gulf, exhibited a dark mid lateral stripe on the flanks.

H. (H.) howesi lives in holes, crevices and gaps among rock boulders, and has never been recorded from other habitats. These stenotopic microhabitat demands restrict the species to rock shores composed of rather big to very big boulders. Only among such are hollow spaces large and plentiful enough to offer suitable conditions for large growing cave-dwellers. The population densities of this species may never have been very high. However, within the past ten years, it almost or entirely disappeared from its type localities in the northern Mwanza Gulf (van Oijen 1992). The last record from the Mwanza Gulf, given as 1992 in van Oijen (1992), is based on a mis-identification. The fishes, van Oijen referred to (as Bouton & Fermon, pers. comm.), were subadults, collected by Y. Fermon and me, that turned out to be a new species (see

A male *H. howesi* from Gana Island.

A territorial male *H*. "orange rock hunter" from Gabalema Islands.



View towards Ukerewe from the plant-covered rocks of Zue Island.

below). The last record of *H. (H.) howesi* in the Mwanza Gulf is from 1989 at Anchor Island (N. Bouton, pers. comm.). However, in early 1996 we found *H. (H.) howesi*, or very similar fishes, at two islands in the Speke Gulf and at Gana Island northwest of Ukerewe. In the Speke Gulf we caught only females. They agree anatomically and with regard to the peculiar fin squamation with *H. (H.) howesi* from the northern Mwanza Gulf. I consider them conspecific, though final security can not be achieved without knowledge of male coloration. At Gana Island we caught a big male and a female. Also these agree with the description, though the scales on the fins are fewer than in Mwanza Gulf and Speke Gulf individuals, and are usually not more than two in a row.

Van Oijen sampled between 0.5 and 2.5 m water depth and got many subadults but very few adults of *H. (H.) howesi*. He assumed that the latter may stay deeper (van Oijen 1992). This may well be the case. At Sozihe and Vesi Islands adult *H. (H.) howesi* live at depths down to at least 7 m. The habitats are moderately to steeply sloping rock shores which are composed of big boulders. At Gana Island the species lives in big caves among huge boulders, and we found adults already at about 2.5 to 3 m depth. Van Oijen (1992) gave extensive information about food and feeding habits of *H. (H.) howesi*: In the northern Mwanza Gulf adults of this species used to prey upon crabs (*Potamonautes niloticus*) and fish (*Haplochromis* and the cyprinid *Rastrineobola argentea*). The biggest haplochromines swallowed by this predator measured over 50 mm standard length. Van Oijen assumes that crabs are not eaten entirely, but that *H. (H.) howesi* is rather a kind of a crab parasite, tearing off limbs which can be grown new by the crab. Subadults used to prey predominantly on fish, furthermore on prawns (*Caridina nilotica*), insect larvae (mostly dragon flies, Odonata) and crabs. The haplochromines eaten, were usually epilithic algae scrapers (*Neochromis* lineage). Already *H. (H.) howesi* of little over 50 mm standard length, in van Oijen's study, preyed upon juvenile haplochromines. The stomach of a female (113 mm SL) from Vesi Islands that we examined, contained a macerated fish that must have had about 15 mm standard length. The intestine contained another fish that was darkly pigmented, and a heap of unidentified invertebrate eggs.

At Hippo Island and Bwiru Point in the entrance to the Mwanza Gulf, we caught a few subadults of *H. (H.) howesi*-like fishes in rocky crevices. Considering the fact that *howesi* is not the only species of its kind in the area, as was previously assumed, we cannot be sure of the identity of these fishes. Though with the new records *H. (H.) howesi* seems geographically more widely distributed than previously known, I consider it critically endangered. At all its recent record places it was very rare.

***Haplochromis (Harpagochromis)* "orange rock hunter"** is the second known species of rock crevice hunters and probably closely related to *H. (H.) howesi*. Some subadults were collected by Y. Fermon and me at Gabalema Islands ("Rocky Islands" in van Oijen 1992) in the Mwanza Gulf entrance. After they had reached adulthood in aquaria, it became evident, that they belonged to a new species, and were not *H. (H.) howesi*. Their general appearance is very similar to that of *H. (H.) howesi* and they share with the latter the squamation of anal and dorsal fin. "Orange rock hunter" differs from *howesi* by a shorter lower jaw and bigger eyes (table 3), but most distinctly by an entirely different male coloration.

Reproductively active males are light grey on the dorsal head surface and the dorsum, and bright orange-red on cheeks, gill cover and flanks below the lateral line. The dorsal fin is metallic blue in the spinous part, transparent with red streaks in the soft part, and has black lappets. The caudal fin is transparent with red streaks and maculae, the anal fin anteriorly pinkish red, posteriorly whitish with light yellow egg dummies that are much bigger than those on the anal fin of male *H. (H.) howesi*. The spinous part of the pelvic fins is black, the soft part pink red. Females are olive-greenish, lighter coloured than those of *H. (H.) howesi*, but otherwise very similar to them. Both sexes bear a prominent melanin pattern, consisting of a mid lateral stripe, an interrupted dorsal lateral stripe, and indications of five or six vertical bars. Various head markings can be prominent in males. The bright coloration, together with the streamlined body shape, give *H. (H.)* "orange rock hunter" a most attractive appearance.

To date "orange rock hunter" is known from just one locality, Gabalema Islands in the Mwanza Gulf entrance. Even there it is extremely rare. Its habitat are crevices among big rocks at a very steeply sloping place. Despite extensive search we never found adult individuals. Like those of *H. (H.) howesi* they may stay at greater depths. "Orange rock hunter" may occur at more places in the Mwanza Gulf entrance. However, the circumstance that usually only subadult individuals are caught, makes the identification difficult. We found at Hippo Island and Bwiru Point subadults that are similar to those from Gabalema Islands. Their identification is pending. I also do not know whether the two species, *howesi* and "orange rock hunter" live or lived sympatrically at the same islands. The circumstance that *H. (H.) howesi* is now known also from the Speke Gulf, and thus from south and north of Gabalema Islands, and that *howesi* and "orange rock hunter" differ in eye size and egg dummy size, indicates that the two species are not merely replacing each other geographically.

I observed a complete sequence of paternal mouthbrooding (three weeks) and guarding of post-buccal stage juveniles (another three weeks) in a male of *H. (H.)* "orange rock hunter". This male was the only wild caught male that has been kept in aquaria until now, and performed brood care only once (Seehausen in prep.).

Crevice-dwelling piscivores are a consistent component of cichlid communities at steeply sloping rock shores in Lake Victoria. It seems quite possible that more, as yet unknown species of this group (*H. (H.) howesi* group) exist in the lake. In view of their rapid decline (*H. (H.) howesi*) and narrow geographical range (*H. (H.)* "orange rock hunter"), the two known species are to be considered critically endangered.

Egg and fry robbers of the *Lipochromis* lineage

Bizarre modes of feeding have evolved in a group of piscivorous haplochromines that, rather than hunting juvenile haplochromines, persecute mouthbrooding females to forcefully deprive them of their brood. Amazingly little is known about the hunting techniques of these so called paedophages ("children eaters"). This is certainly due to the fact that very few of them have been maintained in aquaria yet. Greenwood (1959b) hypothesized that paedophages obtain their prey forcefully by engulfing the snout of brooding females. Fryer & Iles (1972) held against this view the alternative hypothesis that females voluntarily jettison their eggs or young under stressful conditions, and that the young would be eaten then by paedophages. This, they assumed, might be a mechanism enabling cichlid populations to regulate their densities. In the meantime a few behavioural observations on paedophagous feeding behaviour in haplochromines have been made, all supporting the view that paedophagous cichlids obtain their prey by forceful means.

As bizarre as paedophagy may appear to us, its appearance is very common in the evolution of lacustrine radiations of haplochromine cichlids. Paedophagous species are known also from Lakes Edward, George, Kivu, and Malawi (Nyasa). At least those of the latter certainly evolved independently of those in Lake Victoria. Anatomical similarities between the phylogenetically unrelated paedophages of the different lake systems are amazing (compare for instance Greenwood 1959b with Stauffer & McKaye 1986).

Greenwood (1980), in his last revision of the Lake Victoria haplochromines, assigned all anatomically derived

A male *Haplochromis cf melanopterus* from Makobe Island in the aquarium.

These cichlid larvae were taken from the stomach of *H. cf melanopterus*.

An OB *H. cf melanopterus* from Makobe Island.

A mouthbrooding female *H. cf melanopterus* from Makobe Island.

paedophages to the resurrected genus *Lipochromis* Regan, 1920. He defines this lineage as follows. *Haplochromines with a thick-lipped, widely distensible and protractile mouth, and small teeth that are deeply embedded in the oral mucosa (often invisible without dissection). The body depth ranges from 27-47% of the standard length. The lower jaw length lies between 38 and 56% of the head length (modal range 42-48%). The lower jaw is either broadly rounded, almost square shaped or boat-shaped with an anteriorly rapid narrowing, making its outline more acute. The posterior end of the maxilla is bullate, well visible even when the mouth is shut. There are two distinct forms of outer teeth. In one, the tip of the crown is inclined anteriorly or laterally* (a unique feature among Victorian haplochromines;

my words) *whilst in the other it is either vertical or fairly strongly recurved. The inner teeth are arranged in one or two rows and are predominantly unicuspid in large fish* (above 100 mm SL). *Compared with the teeth in equal-sized fish from other lineages, those of Lipochromis are shorter. Moreover, the number of teeth in the outer rows is reduced, the posterior third of the premaxilla* (teeth carrying upper jaw bone) *is devoid of teeth or teeth are present but widely spaced.*

Based on jaw and tooth shape, Greenwood distinguished two subgenera. *Lipochromis* (or *obesus* complex) contains species with a broadly rounded lower jaw (one exception) and outer teeth, the crowns of which are inclined anteriorly. *Cleptochromis* (or *parvidens* complex) contains species with a boat-shaped lower jaw and straight or recurved teeth. By that time, seven species were known and described, four in the first subgenus (one from Lakes Edward and George), three in the other one. In this more recent work Greenwood revised his prior assumption (Greenwood 1974) that the two groups of paedophages would represent two unrelated lineages, that had evolved parallel. Since Greenwood's revision twelve new species of paedophages have been discovered in Lake Victoria, though none of them has been described yet. Greenwood (1980) already observed that the gap in jaw form between the subgenera *Lipo-* and *Cleptochromis* can almost entirely be bridged by some species. Two of the new species from rocky shores add considerably to this. Consequently in the definition of the *Lipochromis* lineage the lower jaw shape should be described as broadly rounded, boat-shaped to almost square shaped. *H. (L.) obesus* and one new species (*H. (L.)* "matumbi hunter") differ distinctly in melanin pattern from the other *Lipochromis* (see below).

A few more words about the peculiar feeding behaviour of *Lipochromis*: Greenwood (1974) observed in an aquarium-kept *H. (L.) parvidens* "behavioural patterns suggesting it might engulf the snout of a brooding female". Wilhelm (1980) observed a male of an undescribed member of the *H. (L.) obesus* group in an aquarium, attacking and chasing brooding females of other haplochromines, that Wilhelm had introduced into the tank. When stressed, most females spat out part of their brood which was eaten up immediately by the paedophage. As long as the females retained some eggs or larvae, the paedophage continued harassing them. After this led to exhaustion of females, the paedophage engulfed their snout with his mouth and sucked out remaining eggs or fry. Wilhelm suggests that the origin of snout-engulfing may lie in a modification of fighting behaviour of a piscivorous ancestor, hunting on already released young that are still guarded by the female. The snout-engulfing, as observed by Wilhelm, appeared to be the climax of a performance which resembled a fight, and usually happened after the female was so exhausted that the paedophage was able to manipulate it.

These are interesting observations that show that snout engulfing, that was hypothesized on basis of the anatomy of paedophages, indeed exists. However, the observations tell relatively little about the importance of such behaviour in nature. A female in nature would likely try to escape as soon as she sees the paedophage, or latest, after it starts to attack her. Thus, it is most unlikely that the paedophage would actually get the possibility to exhaust the female until she cannot resist snout engulfing any more. More likely the paedophage must actually catch the female by surprise, or must engulf her snout in a real fight, in which she is attacking him frontally. This latter passibility seems real, considering the circumstance that brooding females of many littoral haplochromines (all *Mbipi* species of which I observed brooding females) are territorial and quite aggressive. I have observed paedophages in nature, roaming around among the territories of brooding females. Though I have not seen them being attacked by such females, it is possible that this happens once a paedophage tries to enter the hideout of a female.

It seems to me therefore that snout engulfing in nature can function only in a situation, in which the paedophage intrudes into a territory and hideout of a brooding female, thus in littoral and benthic habitats. In situations were brooding females are not territorial, for instance in open water dwelling cichlid species, a hunting technique described by McKaye and Kocher (1993) on paedophages from Lake Malawi, is likely to be the more important one. These authors observed three species of paedophagous haplochromines ramming brooding females in the open water, and in this way forcing them to jettison some eggs or young involuntarily. Many more underwater observations are needed to understand the ecological and evolutionary importance of the different behaviour patterns in paedophages. Observations in large aquaria, however, could certainly contribute a lot. A third strategy of paedophagy, "egg snatching", evolved in another lineage of Lake Victoria haplochromines, and is discussed on page 243.

Greenwood's (1959b) data suggest that most paedophages in Lake Victoria are not very much restricted to particular bottom types. However, with the exception of *H. (L.) melanopterus* (known from a single fish) and *H. (L.) parvidens*, all species were found predominantly over hard bottoms, thus sand, shingle or rock. Most paedophages have become very rare after the Nile perch upsurge and many disappeared entirely. So have *H. (L.) maxillaris*, *H. (L.) microdon*, and at least two undescribed species after 1986 entirely disappeared from former places of occurrence in the Mwanza area (Witte et al. 1992). Most of the currently surviving species are found only at rocky shores and islands. Unfortunately very little is known about their ecology and life history. Thus it is not clear, whether these are local populations that are isolated from each other by stretches of non-rocky bottom and deep water, like many other rock cichlids, or whether more frequent migration exists between localities. There is some evidence that *Lipochromis* species inhabiting rocks are indeed particularly adapted to that habitat type: All species that we found at rocky shores had size reduced and deeply embedded chest scales, while a species of the *H. (L.) parvidens* complex that we caught in a weed bed, had generalized chest squamation. Knowledge about functional population size is an important prerequisite for developing strategies to protect the highly endangered species of the *Lipochromis* lineage. A first step, however, is to know and recognize the species. I hope the information on the following pages will contribute a little to this.

Haplochromis (Lipochromis) melanopterus Trewavas 1928 is one of the taxonomically least studied cichlid species of Lake Victoria. It was described from a single specimen that was caught early this century in the Smith Sound, the southwestern extension of the Mwanza Gulf. It's, for a paedophage unusually short lower jaw, and the combination of an *obesus* complex head shape with a lower jaw shape that resembles more the one found in the *parvidens* complex, caused some reservation about the specific status of the fish (Greenwood 1959b). This in particular, because the specimen had apparently suffered some *postmortem* distortion. Much later (Greenwood 1980) more fishes were found that seemed to fit the description of *H. (L.) melanopterus*. However, details about these have never been published.

We found at rocky shores and islands in the southern Speke Gulf and Sengerema region a paedophage that, with some probability, is *H. (L.) melanopterus*. It has a short lower jaw, though not as short as in the type specimen (compare tables 3 and 4), has a typical *obesus* complex head shape and a lower jaw similar to that of *parvidens* complex species. It narrows rapidly in its anterior half and is pointed. This shape of the lower jaw, and its small length, serve to distinguish *H. (L.) melanopterus* from the otherwise similar *H. (L.) maxillaris*. Other distinguishing characters are a chest and nuchal squamation with size reduced scales in *H. (L.) melanopterus* versus generalized scales in the other species and a higher number of scale rows on the cheek (3-4

The island Sozihe in the Speke Gulf.

A male *H. cryptodon* from Mafwinki Island.

versus 2-3). In all these characters the fishes from rocky habitats in the Speke Gulf agree with the type specimen.

Reproductively active males are very beautiful, but rarely seen. Apparently only large males develop the bright colours. Their head, dorsum and caudal peduncle are dark brown, the underside is grey-brown. Framed by these dark colours, the flanks are bright yellow, interrupted by about seven dark brown-black vertical bars. All vertical fins are dark, the dorsal fin with a metallic blue band in the spinous part, and the anal with some blueish flush and small yellow egg dummies. Females are light brown-grey, with up to eight narrow vertical bars, that are very regular in outline and position. This melanin pattern is reminiscent of the one in the *Mbipi* species of the *Haplochromis nyererei* complex. *H. (L.) melanopterus* has an orange-blotched (OB) morph, similar to those of *Mbipi* species of the *Neochromis* complex.

The type specimen of *H. (L.) melanopterus* was caught over mud bottom. We have never found the species over such bottom, nor in any other habitat apart from rocky shores and islands. We found it living at gently to moderately steeply sloping shores with small to medium sized boulders. We observed adults between 0.5 and at least 6 m water depth, but with higher frequencies in shallow waters. This is the most widely distributed and most frequently encountered paedophage at rocky shores in southeastern Lake Victoria. This notwithstanding, it occurs generally just in very low densities. Quite extensive aquarium observations showed that this species exhibits a far lower level of intraspecific aggression than any other rock cichlid that has been kept in aquaria, except *H. (L.)* "Matumbi hunter". Dominant males are very tolerant of other males and females in all stages of sexual activity. Even brooding females are always accepted in the males territory and are not harassed as in other haplochromines.

Of three individuals whose stomachs we examined, two had empty stomachs, and one had the stomach entirely filled with juvenile *Haplochromis* and a few *Haplochromis* eggs (see photo). Though they had begun to be digested, in some of the juveniles a yolk sac was visible. Thus they must have been eaten in a stage in which they were still in their mothers mouth (buccal stage). I frequently had the opportunity to observe *H. (L.) melanopterus* under water in its natural habitat. In times in which many brooding *Mbipi* females are hiding among rocks and under overhanging shore vegetation at Makobe Island, also the paedophages accumulate in the very shallow water, and are seen roaming slowly around among the *Mbipi*. Aquarium observations learned me that females of *H. (L.) melanopterus* attempt to obtain eggs and fry even from brooding females of their own species, but are never successful. They slowly approach a brooding female from laterally behind and above. When about 10 cm from her mouth, they turn slightly to one side, as if ready to attack. Latest in this moment the brooding female simply turns away. When the harasser is attacked by the brooding female, attacks consist of lateral display and tail beats only. They miss the frontal display and frontal attack component that is otherwise characteristic for haplochromine combat behaviour and is performed in other species also by brooding females. A frontal display and attack would offer the paedophage opportunities to get hold of the mouth of the brooding female. Thus, the avoidance of this component of combat behaviour may be an adaptation, protecting brooding females of *H. (L.) melanopterus* against loss of offspring through the feeding mode of its own species. The defence behaviour of brooding *H. (L.) melanopterus* females shows with what simple means a paedophage can be disarmed.

H. (L.) melanopterus lives in sympatry with *H. (L.) cryptodon* and possibly with *H. (L.)* "velvet black cryptodon" but is easily told apart from both on basis of body and head shape, and coloration.

Haplochromis (Lipochromis) cryptodon Greenwood 1959 is according to Greenwood the anatomically least specialized among the described *Lipochromis* species. Greenwood (1959b) observed a very patchy distribution of the species, which he could not explain on grounds of habitat choice. Though he does not explicitly state so, the predominant habitat seems to have been sandy bottom. Witte et al. (1992) found *H. (L.) cryptodon* or a very similar species (*H.* "black cryptodon") in the pre-Nile perch times over a mud bottom in the Mwanza Gulf. In the 1990s we found *H. (L.) cryptodon* only at gently to very gently sloping rocky islands.

The taxonomic identity of *H. (L.) cryptodon* is problematic because the coloration of living males was not known to Greenwood and is thus lacking in the species description. Because of this uncertainty the *cryptodon*-like fishes from the Mwanza Gulf were usually referred to as "black cryptodon" (Witte et al. 1992). However, the colour of preserved males from rocky shores agrees quite well with that described by Greenwood for preserved males of *H. (L.) cryptodon*. They are not black (unlike those of *H. (L.)* "velvet black cryptodon") but dark grey-brown. Greenwood included in his description four fishes that differed from the others by being more slender (27.5-31 % of the standard length). Since these fishes were amongst the smallest individuals, he considered the slender body a "juvenile" character. All our individuals belong to this slender type, and are in size indeed at the lower end of the range of individuals used by Greenwood for the description of *H. (L.) cryptodon*. Nevertheless, it can at present not be excluded that the current definition of *H. (L.) cryptodon* includes more than one species.

Males of *H. (L.) cryptodon* from rocky habitats are dark grey-black on the head, dorsum and underside, while the flanks are slightly lighter grey with greenish to blueish metallic flush. The overall impression, nevertheless, is that of a grey-black bodied fish. The dorsal fin is black with red lappets and some red maculae, the caudal fin is largely bright red, and so is the anal fin, which carries usually two large yolk-yellow egg dummies on red ground. The pelvic fins are black and the pectoral fins have a red flush. We have not yet seen females but Greenwood (1959b) describes them as dark green-brown, shading to light gold ventrally. The combination of coloration and slender, streamlined body shape gives *H. (L.) cryptodon* a very conspicuous and beautiful appearance. At rocky islands it has been recorded at water depths ranging from 1.6 to 5 m, at places with medium sized to small rock boulders, but is extremely rare.

Similar and probably closely related to *H. (L.) cryptodon*, but at the same time very distinct, is ***Haplochromis (Lipochromis)* "velvet black cryptodon"**. We discovered it in early 1996 and know it from only one place. It may however, be more widely distributed east of our survey area. This species is distinctly bigger than rock-dwelling *H. (L.) cryptodon*, but as slender as the latter. It has a broader lower jaw than any other species of the *parvidens*-group, and bridges in this respect the gap between that group and the *obesus*-group. *H. (L.)* "velvet black cryptodon" differs in coloration from *H. (L.) cryptodon* as described by Greenwood, and as described above from rocky islands: Males are entirely velvet black, literally from head to tail, including all fins. Sometimes some red streaks exist in the caudal fin and the pelvics can have a flush of red. The egg dummies on the anal fin of the males are more, much smaller and darker than in *H. (L.) cryptodon*. They are dull orange-yellow instead of light yolk-yellow. Preserved individuals retain a deep velvet black coloration, a rare condition among Lake Victoria cichlids. It is known from a few *Mbipi* species, but even those hardly reach the deep saturation of the black displayed by this paedophage. "Velvet black cryptodon" also shares a beautiful orange blotched (OB) morph with those *Mbipi*. The only female that is known yet, is an individual of this OB morph. *H. (L.)* "velvet black cryptodon" has short, stout, slightly recurved outer teeth that are so deeply embedded in the oral mucosa that they are frequently not visible.

This attractive fish lives closely inshore at water depths ranging from 3 to at least 7 m. The rock boulders in its habitat are of moderate to large size, and the slope is partly moderate, partly steep. It is the only paedophage that we found at that place, though *H. (L.) melanopterus* may occur in the low densities that are usual for this species. *H. (L.)* "velvet black cryptodon" seems to behave more aggressive than *H. (L.) melanopterus* when kept in aquaria.

In the northern Mwanza Gulf we found a single female of another undescribed paedophagous species that is anatomically close to *H. (L.) cryptodon* and *H. (L.) melanopterus*, and thus, bridges the gap between the two groups of described paedophagous species. It has a shorter and broader lower jaw than have *H. (L.) cryptodon* and *H. (L.)* "velvet black cryptodon", which, however, is anteriorly rapidly narrowing. Its dorsal head profile is of the *obesus*-group type but its dentition, recurved unicuspid outer teeth in both jaws, of the *parvidens*-group type. Without knowledge of male coloration it is difficult to judge whether this species is identical with one of several undescribed paedophages that are known from sublittoral mud bottoms, or whether it represents another rock-dwelling species. Its chest squamation is of the type, found in all the other paedophages from the rocks and not of the type found in *H. (L.) parvidens*. It lives at a moderately steep slope, in a medium boulder size habitat and we caught it at about 2 m water depth.

Discovered just in 1995, ***Haplochromis (Lipochromis)* "blue microdon"** is probably the most rare of the *Lipochromis* species currently inhabiting rocky shores in south-eastern Lake Victoria. With its incurved dorsal head profile, oblique mouth and relatively narrow lower jaw, "blue microdon" is among the rock-dwelling *Lipochromis* species most distinct. It resembles anatomically *H. (L.) microdon* (Blgr.) 1906 of the *parvidens* group, but has a slightly shorter and narrower lower jaw (table 3 versus table 4). This deviation could be due to the relatively small size of the only individual that we collected and measured, but its coloration is distinctly different from that of *H. (L.) microdon*. Its dentition consists in the outer row of two types of teeth. A rather slender type with orange crown is recurved, while a stouter type with white crown is upright, and the crowns frequently broken off.

Live coloration of *H. (L.) microdon* was not known to Greenwood when he described the species. However, it was described later by M. van Oijen in a paper of Greenwood & Barel (1978). According to that paper and unpublished photographs (Witte pers. comm.), males of *H. (L.) microdon* are grey and yellowish with an extensive coppery to bright red area behind the pectoral fins, somewhat reminiscent of *H. (Paralabidochromis)* "rockkribensis". Such fishes were not caught over rocks. Our male from a rocky shore was metallic light blue on the entire flanks, with orange-yellow anal fin, caudal fin, and dorsal fin lappets, and with orange-yellow egg dummies. While more than five mud, sand and rock-dwelling paedophages are known that anatomically resemble *H. (L.) cryptodon*, "blue microdon" seems to be the first new species resembling *H. (L.) microdon*. We found it in shallow water at a gently sloping shore with small rock boulders in the northern Speke Gulf. Frans Witte (pers. comm.) had seen similar fishes in the Speke Gulf before the Nile perch boom.

***Haplochromis (Lipochromis)* "matumbi hunter"** is the most peculiar among the new species of the *Lipochromis* lineage and one of the most peculiar of all the new rock-dwelling haplochromines. It is the combination of an unusually slender body, reminiscent of pelagic zooplanktivores, with an *obesus*-group "pug head" and an, among rock-dwelling cichlids very rare melanin pattern, that creates this peculiar impression. However, the peculiarities are more and include dentition. The teeth of "matumbi hunter" are less deeply embedded than in other species of the lineage and those in the outer rows, particularly in the lower jaw, can be rather long and slender. In spite of this, the outer teeth of the lower jaw are distinctly inclined rostrad like in other members of the *obesus*-group. Those in the upper jaw

A territorial male *H. cryptodon* from Makobe Island.

A male *H*. "velvet black cryptodon" from Sozihe Island.

An OB female of *H*. "velvet black cryptodon" from Sozihe Island.

H. "Matumbi hunter" in the aquarium.

A male *H*. "blue microdon" from Zue Island.

A male *H*. "Matumbi hunter" from Matumbi Island.

are upright or slightly recurved. The inner teeth are unicuspid even in fishes of below 100 mm SL. The lower jaw is narrower than in other species of the *obesus*-group but not anteriorly narrowing as rapidly as in the species of the *parvidens*-group. *H. (L.)* "matumbi hunter" shares with *H. (L.) obesus* a melanin pattern of a continuous and very broad mid lateral stripe. I did not see such a stripe in any other *Lipochromis*, nor in any other rock-dwelling cichlid. This may indicate a close phylogenetic relationship between the two species. The chest squamation of "matumbi hunter" is a typical rock cichlid squamation with small and deeply embedded scales.

H. (L.) "matumbi hunter" is known from a single, topographically very narrowly restricted place in the southern Mwanza Gulf. It is most likely that its occurrence there is a remnant of a once more wide spread distribution, and I consider it to be one of the most critically endangered cichlid species at the rocky shores in southern Lake Victoria. Its habitat is shallow water (1 to 2 m depth) over large, but only moderately steep rock boulders. This is a rare habitat situation, since large boulders mostly slope steeply. Peculiar habitat demands may contribute to the rarity of this species, though one would see little reason for a paedophage to be that narrowly habitat specific. It may, however, be that this species depends more than other paedophages on a mixed diet. We studied the stomach contents of two individuals. One had eaten predominantly fish eggs (probably of haplochromines), and to smaller amounts may fly (Ephemeroptera) larvae and zooplankton (Cladocera). The other one had eaten only may fly larvae (predominating) and zooplankton.

We were lucky enough to build up a breeding stock of this unique species and one can hope that aquarium observations will contribute to an understanding of the ecological significance of its peculiar morphology. Like *H. (L.) melanopterus* also this species exhibits very little intraspecific aggression. Females, while guarding their fry, make an exception to this. Among the species of Lake Victoria haplochromines that I have been breeding in aquaria, "matumbi hunter" behaved exceptional in that it hardly preyed upon fry of its own species. Fry grew up in the midst of a group of adults.

A real curiosity is a fish that is known from only a single big male. On first glance it is a *Haplochromis nyererei*, closely resembling the males of the population with which it lives sympatrically. Just when looking a second time we realized that the fish has an *obesus*-like "pug head" with a snout that is much broader than in any normal *H. nyererei.* Further inspection of the fish revealed that its anterior outer teeth are stouter than in *H. nyererei* and that outer and inner teeth are deeply embedded in oral mucosa. Moreover, the last part of its premaxillae is free of teeth, apart from one tooth on the left side. Sympatric males of *H. nyererei* have their teeth distributed in regular distances over the entire length of the premaxillae. Thus, anatomically the pug-headed fish is a typical paedophage. I would still consider it a morphologically aberrant individual of *H. nyererei,* were differences restricted to characters of jaws and teeth. However, the egg dummies of the "pug-head" are bigger than in any known species of the *H. nyererei* complex and almost twice as big as in individuals of the sympatric population of *H. nyererei* (3.64 +/- 0.39 mm versus 1.88 +/- 0.16 mm diameter, excluding the transparent outer ring). It appears not plausible why an individual of *H. nyererei* that has an aberrant (paedophage like) jaw structure, oral mucosa and dentition, should also have an aberrant egg dummy size. Rather it may represent a paedophage in *H. nyererei* dress. It could either be a morph or species of the *H. nyererei* complex or a *Lipochromis* that has adopted the coloration of *H. nyererei*, possibly mimicking the males of its prey species. Until more is known I call it ***Haplochromis (?)* "nyererei paedophage"**.

Silver arrows of the "Double stripe" complex

Anatomically very different from all other rock-restricted cichlid species are the members of a "new" species complex that has recently been described by Van Oijen & Witte (1996), and for which no (sub)generic name is available yet. These are tiny and very slender insect- and zooplankton eaters, probably closely related to ***Haplochromis (?) diplotaenia*** Regan & Trewavas 1928. *H. diplotaenia* has long been a "forgotten" species until van Oijen & Witte redescribed it. It is known from a single female that was caught in Uganda. Regrettably ecological information is not available, neither about its habitat, nor about its diet. *H. diplotaenia* has a characteristic melanin pattern of two dark, thin longitudinal bars (mid lateral and dorsal lateral stripe) on silvery whitish ground. Similar fishes have been exported from Uganda to Sweden under the name *Prognathochromis sp. aff. longirostris* by B. Selbrink in the 1980s (Selbrink 1985b). Similar fishes have also been observed in the southern Tanzanian part of the lake since 1978, and were referred to as *H.* "double stripe" (Witte et al. 1992, Seehausen 1995b, Seehausen & Witte 1995). The recent taxonomical study demonstrates that the southern "double stripe" comprises two species, both of which are specifically distinct from *H. diplotaenia.* The two species differ most markedly in habitat and diet.

Before the Nile perch became abundant, one of them, ***Haplochromis (?) tanaos*** van Oijen & Witte 1996, inhabited sand bottoms. It is dealt with here only because of its great resemblance with the other one. ***Haplochromis (?) thereuterion*** van Oijen & Witte 1996, was observed exclusively over rocks. Though some morphometric differences between the two species exist (see van Oijen & Witte 1996), females and quiescent males look very similar. Quiescent males of both species are dorsally blue-grey with some red in dorsal and caudal fins, a red anal fin, and black pelvic fins. When sexually active, those of *H. thereuterion* get a pitch black head and body, and most fins are also black, though the caudal fin has a red margin, and the anal fin is partly red. In contrast, males of *H. tanaos* become dark bluish dorsally, and black on the entire ventral half of the body. *H. thereuterion* has slightly larger teeth than *H. tanaos*, and the outer ones in the lower jaw are somewhat procumbently implanted. Finally, *H. thereuterion* differs from *H. tanaos* by having the premaxilla (upper jaw bone) slightly laterally expanded (visible when the fish is viewed from dorsal, as a slightly convex, rather than a straight snout outline) and slightly thickened lips.

H. thereuterion is known only from the northern Mwanza Gulf. It lived at rocky patches of mainland shore and at rocky islands, being recorded from the Nyegezi Rocks, Nyegezi Bay, Anchor, and Hippo Islands. The one individual from Hippo Island in the north-western Mwanza Gulf differed from those from the eastern Mwanza Gulf localities in morphometrics and coloration, possibly suggesting restricted gene flow between populations across the Mwanza Gulf (van Oijen & Witte 1996). *H. tanaos* is known from several places along the entire southern shore of Lake Victoria. Both "double stripe" species have declined dramatically after the Nile perch upsurge. The two lived (past tense! See below) at some places parapatrically, e.g. in the Nyegezi Bay. The rock-dwelling *H. thereuterion* occurred more inshore than the sand-dweller. Though being confined to rocky substrates, it is, in contrast to most other rock cichlids, not a bottom oriented fish, but seems to be more surface oriented. It feeds predominantly on terrestrial insects which it apparently collects from the surface. Furthermore it eats chironomid larvae. The sand-dwelling *H. tanaos* used to feed predominantly on zooplankton and insect larvae in the pre-Nile perch era (op. cit.). The great similarity in anatomy and male coloration, and the ecological differences among these species may indicate a recent speciation event, in which diverging habitat (substrate) affinities may have played a

A male *H*. "nyererei paedophage" from western Mwanza Gulf.

A female *H. thereuterion* from Kissenda Island.

major role.

For many years after the Nile perch upsurge, neither of the two species was seen. However, in January 1996 we caught one female of *H. thereuterion* at Kissenda Island in the north-western Mwanza Gulf. Hence there is some hope that this species is surviving, though in extremely low densities. About two years earlier, we found a population of what seems to be a remnant stock of *H. tanaos* in the sublittoral waters of the Kissenda Bay over a mud bottom (Seehausen & Witte 1995, van Oijen & Witte 1996, Seehausen et al. in press [b]). This population had not only changed its habitat but also its diet considerably, feeding now predominantly upon insect larvae. This instance indicates how rapidly adaptation to new ecological demands can occur. *H. thereuterion* is by its melanin pattern easily told apart from pelagic zooplanktivores that occasionally enter into rocky habitats, and that have merely one, if any visible lateral stripe (see pages 256 and 257).

Teeth like a scalpel — algae scrapers of the *Haplochromis* lineage

Dental specialization for scraping algae has evolved among Lake Victoria cichlids along at least two pathways with quite different results. One type of algae scraper dentition is represented by the *Neochromis* lineage (page 66). The sec-

A male *H. tanaos* from the southern part of Lake Victoria.

A female *H. tanaos* collected at Juma Island.

ond type is characterized by bicuspid or unicuspid teeth with a compressed crown, and a major cusp that is laterally strongly expanded (protracted) to form a broad scalpel-like scraping surface. In his last revision, Greenwood (1979) restricted the genus *Haplochromis* Hilgendorf, 1888 to species with such tooth form. At least 17 are known from Lake Victoria (Witte et al. 1992, Kaufman & Ochumba 1993, Seehausen et al. in press [b]), of which merely two are described. One more is described from Lake Nabugabo (*H. (H.) annectidens*), an eastern satellite of Lake Victoria, one from Lakes Edward and George (*H. (H.) limax*) and one from Lake Kivu (*H. (H.) astatodon*). I refer to them here as to the *Haplochromis* lineage (*sensu stricto*).

While the *Neochromis* dentition type is restricted to fishes living in rocky habitats, and is among them apparently very successful, the *Haplochromis* dentition type is found predominantly in habitats with submerged vegetation, e.g. water-lily zones and floating reed mats. However, it occurs in a few species also in rocky habitats. Greenwood (1956a) noted that the two by then known species with *Haplochromis* dentition, *H. (H.) obliquidens* and *H. (H.) lividus*, inhabited vegetation rich areas as well as rocky piers. Though both are known from south-eastern Lake Victoria, they are there largely restricted to vegetation, and therefore only briefly introduced in my species account. However, at least three other species are regularly or exclusively found at rocky shores.

Many species of the *Haplochromis* lineage (*sensu stricto*) feed primarily on diatoms which they scrape off submerged leaves and stems of plants, and off rocks. To scrape off diatoms from leaves, the fishes take, according to Greenwood (1981), a leaf in the mouth and, holding it loosely, swim along its length, scraping off the epiphytes as the leaf passes between the teeth. Greenwood assumes that the peculiar tooth shape is an adaptation to this way of feeding. Nevertheless, the rock-dwelling species engage heavily also in "rock-scraping". As a consequence, their tooth crowns are usually strongly abrased. It may be interesting to note here that teeth of the *Neochromis* dentition type hardly ever show traces of abrasion, and in this way prove to be more durable in rock-scraping.

Greenwood (1979) defined the genus *Haplochromis (sensu stricto)* as *haplochromines that have the crowns of their outer jaw teeth compressed and noticeably expanded relative to their slender, cylindrical neck and body. The major cusp in bicuspid teeth is very much larger than the minor one. The compressed, anteriorly protracted and dorsoventrally expanded major cusp gives the tooth, be it bi- or unicuspid, the appearance of having an obliquely truncated crown. The number of rows of inner teeth in both jaws lies between 4 and 6* (but between 2 and 6 according to Greenwood's (1956b) species descriptions)*. The inner teeth are tricuspid, but in some species the anterior and anterolateral teeth in the outermost one of the inner rows may be identical with those of the outer row. All jaw teeth are moveably implanted.*

Most of the new species with *Haplochromis*-like dentition from rocky habitats can unambiguously be assigned to the so defined *Haplochromis* lineage. Apart from tooth shape there is currently little evidence for the monophyly of the lineage. The species regularly encountered at rocky shores show either no distinct melanin pattern or one of vertical bars and a faint midlateral stripe. Greenwood (1980) considers the *Haplochromis* lineage to be closely related to the *Neochromis* and *Xystichromis* lineages. Support for this view has recently come from a study of squamation characters (Lippitsch 1993). In that case, it is likely that *Haplochromis* is a close relative, maybe the sister group (?) of the whole complex of "vertical bar *Mbipi*".

Haplochromis (Haplochromis) obliquidens Hilgendorf, 1888 was the first cichlid to be described from Lake Victoria. It has been recorded from various places along the lake shore and even from the very isolated rocky Godziba Island in the centre of the lake. However, since not of all these populations male coloration is known, it remains to be investigated whether they actually represent the same species. *H. (H.) obliquidens* is characterized by a unique tooth shape that it shares, among the known species, only with *H. (H.)* "blue obliquidens", and which represents the most derived condition (= most far removed from the basic haplochromine tooth shape) within the *Haplochromis* lineage. The anterior teeth in the outer tooth rows have on slender necks obliquely truncated crowns, on which the minor cusp is entirely lacking so that the tooth is unicuspid, resembling a curved scalpel. Males are bright yellow-green, with a yellow-grey dorsal fin with red lappets and maculae, an anal fin with some pinkish flush and yellow egg dummies, and pelvic fins that are half black and half faint pinkish. Females are silvery-yellow, with yellow anal and pelvic fins.

Though the combination of tooth shape and male coloration should make *H. (H.) obliquidens* easy to identify, its name has many times been used in aquarium literature for yellowish haplochromines with different dentition. In most cases these were *H. (?)* "thick skin"-like insect eaters. *H. (H.) obliquidens* is a shallow water dweller that has been observed in the vicinity of emergent vegetation, in water-lily zones, at the margin of papyrus swamps, but also over sand and rocky substrates (Greenwood 1956b, Katunzi 1980, Witte & Witte-Maas pers. comm.). At least in the Mwanza area it has become very rare recently. I have personally never seen it alive, and unfortunately cannot show it in a photo. *H. (H.) obliquidens* feeds predominantly upon diatoms and detritus, but at least occasionally also on large amounts of insect larvae (Greenwood 1956b, Katunzi 1981).

Anatomically very similar to *H. (H.) obliquidens* is the rock-dwelling ***Haplochromis (Haplochromis)* "blue obliquidens"**. It has the typical *obliquidens* tooth shape and differs from that species predominantly in male coloration, has smaller eyes and small, deeply embedded chest scales, like the majority of rock-dwelling haplochromines. Males are bright light blue on head, dorsum and flanks. The dorsal fin is light blue with orange coloured lappets and orange-red maculae in the soft part. The caudal fin is bright orange to red, the anal fin yellowish-orange with relatively large yellow egg dummies. Females are silvery grey with transparent fins. Both sexes exhibit between 6 and 8 vertical bars on the flanks.

H. (H.) "blue obliquidens" is known only from Makobe Island in the south-western Speke Gulf. It seems to be very specific in its microhabitat choice, being found only inshore, at places that are slightly protected against the surf by offshore rocks, and usually are near to some grassy vegetation, hanging into the water. We never saw it at water depths beyond 2 m. It shares its habitat with several other algae scrapers of the *Neochromis, Xystichromis* and *Haplochromis* (*H. (H.)* "purple yellow") lineages. The brightly coloured males have their territories on the rock surface. In aquaria they defend their territories quite aggressively. I frequently observed "blue obliquidens" scraping algae from the small and medium sized rock boulders in the shallow water. Its outer teeth are usually strongly abrased. They seem to be pulled over the rocks in such an angle, that the abrasion shapes the originally obliquely truncated teeth again obliquely truncated. Of three individuals that we examined, one had eaten predominantly moss animals (Bryozoa) and in smaller amounts diatoms and blue-green algae. The other two had eaten almost exclusively may fly larvae (Ephemeroptera) and some caddis fly larvae (Trichoptera). The stomachs of all three contained also some fragments of plant tissue. *H. (H.)* "blue obliquidens" seems to be an opportunistic feeder just like *H. (H.) obliquidens*. Unlike in the *Neochromis* algae scrapers, that live sympatrically with it, both sexes are found at about equal frequencies.

The second described Victorian species of this lineage, ***Haplochromis (Haplochromis) lividus*** Greenwood 1956, has a less extreme tooth shape. Even in the anterior-most teeth, the minor cusp is still present and the major cusp is less protracted. Furthermore it differs from *H (H.)*

A male *H.* "blue obliquidens" from Makobe Island.

obliquidens and *H. (H.)* "blue obliquidens" in male coloration. Males have light olive-green ground colour and a golden-red flush on the flanks, extending from the head to the caudal peduncle according to Greenwood (1956b). The fishes that we found in the Mwanza Gulf half bright orange-red flank coloration that extends

A mouthbrooding female *H*. "blue obliquidens".

A male *Haplochromis lividus* from Nyegezi Rocks.

A male *H*. "purple yellow" from Nyegezi Rocks.

A male *H*. "purple yellow" from Kissenda Island.

from the gill covers and dorsal aspects of the head to near the caudal peduncle. The dorsal fin is greyish with red streaks and lappets. The caudal fin is similarly coloured with a red margin. The anal fin is pale greyish with pink flush and rather big yellow egg dummies, the pelvic fins are either entirely black, or half black and half whitish transparent. Females are greyish with yellow anal and pelvic fins.

H. (H.) lividus is known from various places along the lake shores, but again, I consider the taxonomy of these populations unresolved until male coloration is known of all. Greenwood (1956b) found it in shallow littoral zones in the vicinity of emergent and submerged vegetation, in water-lily zones, at the margin of papyrus swamps, and commonly over rock formations of piers. He found it sympatrically with *H. (H.) obliquidens* and had indications, that it lives predominantly in slightly deeper water than the latter. We found *H. (H.) lividus* a few times at rock-reed interfaces in the northern Mwanza Gulf but I consider it there merely an occasional intruder in rocky habitats. Unlike the undescribed rock-dwelling members of the *Haplochromis* lineage, this species has generalized chest squamation. The scales are big and not deeply embedded. Its major habitat probably are areas with submerged vegetation. The species is in south-eastern Lake Victoria not very common.

Much more common is ***Haplochromis (Haplochromis)* "purple yellow"**, a species with a *lividus*-type tooth shape that grows bigger than all other known species of this lineage. It has first been collected by F. Witte & E. Witte-Maas (Witte et al. 1992). Its outer teeth are either bicuspid with a broadly flanged major cusp, or weakly bicuspid with a reduced minor cusp and an obliquely truncated major cusp. Its inner teeth are in the upper jaw, more than in the other species, arranged in a broad band. Males of this species have a very distinct coloration, that can be confused only with that of *H. (H.)* "red back scraper". Their upper head surface, the dorsum above the lateral line and the dorsal fin are dull purple to bright purplish-red. The entire remaining parts of head and body are bright yellow to greenish-yellow. Rock-dwelling males can have a dark sooty-grey underside. The dorsal fin carries in the upper half of the spinous part a distinct metallic light blue band, sharply contrasting with the purplish red of the rest of the fin. The caudal fin is greyish, with dull red streaks and maculae, and a blueish sheen in its lower half. The blueish grey anal fin has a pinkish flush and carries quite many medium sized yellow egg dummies. The pelvic fins are black. Females are light yellowish grey, and both sexes carry between 6 and 8, usually very faint vertical bars on the flanks. The chest scales are not as small as in *H. (H.)* "blue obliquidens" and most other rock cichlids but are somewhat size reduced. They are not deeply embedded.

H. (H.) "purple yellow" is abundant in water-lily zones and at the edge of papyrus stands, but occurs also in purely rocky habitats, including islands that have no submerged or floating vegetation at all. In south-eastern Lake Victoria it is at rocky shores the most frequently encountered, and most widely distributed species of the *Haplochromis* lineage. However, it is never very abundant at rocky shores, and always less abundant than the epilithic algae scrapers of the *Neochromis* lineage. It is entirely absent from most rocky places in the Speke Gulf. At rocky shores *H. (H.)* "purple yellow" lives in shallow water at gently, moderately and steeply sloping shores with all boulder sizes. We never found it at depths beyond 2 m. It is most frequently encountered where reed grows among the rocks at the waterline, and under floating carpets of the water hyacinth (*Eichhornia crassipes*) (Seehausen, Kangwe & Samwel-Terry 1996). In the clear waters at Makobe Island I have observed flocks of *H. (H.)* "purple yellow" grazing epiphytes from the roots and stems of overhanging reed. A male from Nyegezi whose stomach we examined, had eaten predominantly plant tissue and diatoms. At Makobe I also observed them scraping algae from rocks. That this is a common feeding behaviour of rock-dwelling populations, is witnessed by frequent strong abrasion of the outer teeth. The abrasion shapes the teeth less obliquely truncated than in *H. (H.)* "blue obliquidens" from the same place.

***Haplochromis (Haplochromis)* "red back scraper"** is surprisingly similar to *H. (H.)* "purple yellow" in male coloration, but is anatomically quite different. It has a longer head than other species of the lineage, a more decurved dorsal head profile than "purple yellow" and fewer inner tooth rows in the upper jaw (table 3). The shape of the outer teeth is of the *lividus*-type. Males have the same colour bipartitioning of the body that was above described for *H. (H.)* "purple yellow". However, the upper head, dorsum and dorsal fin are more orange-red than purplish. The remaining body is yellow. The dorsal fin has the same metallic light blue band that the fin of "purple yellow" has, and also the other fins are very similar in coloration to those of that species. The metallic blue in the lower half of the caudal is brighter and the anal fin is entirely metallic blue. Females usually exhibit a mid lateral stripe and traces of a dorsal lateral stripe. Both sexes have 6 to 8 vertical bars on the flanks. The chest scales are rather small and usually deeply embedded.

H. (H.) "red back scraper" is known only from a rock-reed interface in the Nyegezi Bay (northern Mwanza Gulf) where it lives in sympatry with *H. (H.)* "purple yellow". It was collected by Y. Fermon and me in 1991 and has not been seen after that. An aquarium population exists, going back to the fishes collected in 1991. Unfortunately not enough is known about the ecology of "red back scraper", to discuss the resemblance in male coloration between this species and "purple yellow".

The last species of the *Haplochromis* lineage that is regularly encountered at rock shores, has a very long, unhandy, but nevertheless descriptive working name: ***Haplochromis (Haplochromis)* "orange chest silvery scraper"**. Its tooth shape is of the *lividus*-type, bicuspid with strongly broadened major cusp. Its head is, relative to the standard length, longer than in all other species, except *H. (H.)* "red back scraper". Its straight dorsal head profile is less steep than that of the latter species. This is a very inconspicuous fish. Males are light silvery greyish with a flush of orange behind and above the pectoral fins. When sexually active, the dorsum gets a beautiful violet flush and the flanks caudad of the orange area become greenish. The silvery overall appearance of the fish is due to the flank scales having a metallic iridescent margin. The fins are greyish transparent to sooty, the anal fin carries two or three orange-yellow egg dummies. Females are greyish-silvery. Both sexes bear about 5 to 7 very faint vertical bars on the flanks and can have a trace of a mid lateral stripe.

"Orange chest silvery scraper" is known from several rocky islands and mainland shores in the central Mwanza Gulf, but is at all of these places rather rare. Only at one place we found this species sympatrically with *H. (H.)* "purple yellow". At three other record localities of "orange chest silvery scraper" we could not find *H. (H.)* "purple yellow", which is otherwise widely distributed in the Mwanza Gulf. This may indicate some sort of ecological segregation between the two species. "Orange chest silvery scraper" lives only in very shallow water, between less than one and maximum 2.5 m depth, and usually at places where reed grows among the littoral rock formations.

Anatomically unspecialized haplochromines of the *Astatotilapia* type

When Greenwood revised the haplochromine species flock of Lake Victoria, a number of species could not be assigned to any of the lineages that he allotted generic rank, due to the lack of any of the derived characters of those lineages. He placed those of them, that were anatomically unspecialized, and not much different from the fluviatile haplo-

A territorial male *H*. "red beck scraper" from a rock-reed interface in the Nyegezi Bay

A female *H*. "red back scraper" from Nyegezi Bay.

A male *H*. "orange chest silvery scraper" from Nansio Island.

The floating water plant *Eichhornia* found in the rocky habitat at Marumbi.

chromines of eastern Africa, together with the fluviatile species into the genus *Astatotilapia* Pellegrin, 1903 (Greenwood 1980). However, he was not satisfied with this solution, for two reasons: (1) The members of the genus *Astatotilapia* share no derived character which would set them apart as a group from the other lineages. In fact, all they share seems to be the absence of the derived characters that characterize other lineages. (2) The species endemic to Lake Victoria (or most of them) differ from the fluviatile species in a number of meristic characters: They have on average more caudal vertebrae (modal numbers 16 *cf.* 15) and more scales along the lateral line (modal numbers 32-33 *cf.* 28-30). Hence Greenwood considered it uncertain whether his *Astatotilapia* lineage was a monophyletic, and thus phylogenetically meaningful, group.

More recently it has been shown on the basis of squamation characters that the lineage is indeed at least diphyletic. Species from Lake Victoria turned out to be closer related to other members of the Victorian flock, than to the river-dwelling *Astatotilapia* (Lippitsch 1993). Greenwood's data on vertebrae and scale counts had indicated this already. All other Lake Victoria haplochromines have vertebrae and scale counts similar to those of the lake-dwelling "*Astatotilapia*". Greenwood, however, had not given these characters much value. He was in uncertainty about whether the differences that he found, were the result of shared ancestry, or merely of eco-phenotypic responses to life in lakes versus life in rivers. However, the correlation between meristic values and habitat is incomplete. At least one species that meristically belongs to the river-dwelling group, lives in typical lake environments in Lake Victoria (see below). This suggests that the meristic differences between the two groups are not the result of eco-phenotypic responses. I think *Astatotilapia* has to be restricted to the predominantly riverine group which, however, has a representative in Lake Victoria. I follow here Lippitsch (1993) to leave the others as "*Astatotilapia*" in quotation marks until their phylogenetic relationships have been identified. To express the distinctiveness of the riverine *Astatotilapia* (including its lacustrine representative) from the endemic lacustrine lineages of Lake Victoria, I do not include *Astatotilapia* among the lineages provisionally treated as subgenera of *Haplochromis* but as a distinct genus.

With this alteration, the *Astatotilapia* lineage is defined after Greenwood (1979, 1980), as *small to medium sized haplochromines with relatively deep body (35-40% of standard length), and predominantly unequally bicuspid outer teeth in fishes of less than 70 mm standard length, that are firmly (not moveably) attached to the bone and the crowns of which are neither much compressed nor clearly demarcated from the neck of the tooth. Some unicuspid teeth are present in fishes of all sizes. They dominate in larger individuals. The scales on the chest are not strongly size reduced, and there are usually between 28 and 30, but never more than 33 lateral line pore scales* (= scales that carry a pore of the lateral line). Lake-dwelling (lacustrine) species of "*Astatotilapia*" fit into this definition, except that they have a higher modal number of lateral line pore scales.

Relatively few anatomically unspecialized haplochromines live at rocky shores. The most frequently encoun*tered species is* ***Astatotilapia nubila*** (Blgr.) 1906. It is widely distributed along the lake shores and is one of the few haplochromine species of Lake Victoria that are not endemic to the lake. It lives also in Lakes Nabugabo, Kyoga and in rivers in the Victoria basin. However, it needs more investigations to confirm that all the populations, that were identified as *A. nubila,* really belong to one species. *A. nubila* is usually regarded the prototype of a generalized haplochromine and is thought to be morphologically close to the founding ancestor of the species flock. This is indeed, among the lacustrine species that I studied, the only one with less than 32 (28-31) lateral line pore scales, and is, at least in this respect, a member of the riverine *Astatotilapia*. From other generalized rock-dwelling haplochromines, it is distinguished furthermore by its rather long head (tables 3 and 4), by large and not deeply embedded chest scales, and by pelvic fins, the first rays of which are prolonged into a distinct filament in males, sometimes also in females. Males are dark green-grey to almost black, with a black dorsal fin that can have red lappets, a caudal fin that is red in its distal third or half, a red anal fin with yellow to orange coloured egg dummies and black pectoral fins. Females are rather light yellow-grey. In both sexes faint traces of about six vertical bars can be visible on the flanks. The outer teeth are upright bicuspids. Those in the upper jaw are sometimes somewhat scraper-like with a small flange, while those in the lower jaw have no flange.

Possibly because of the lack of derived or peculiar characteristics of *A. nubila*, many generalized haplochromines the coloration of which roughly agrees with that given in the description of *A. nubila*, have been identified as that species. In fact quite a number of different species have been regarded as *A. nubila* by aquarists. However, confusion with similarly coloured Lake Victoria species can be avoided by a simple count of the lateral line pore scales.

We found rock-dwelling populations of *A. nubila* only in the Mwanza Gulf and particularly often at steeply to very steeply sloping shores, composed of large rock boulders. They live inshore at water depths ranging from 1.5 to at least 8 m. Population densities can locally be rather high, but usually this species is not among the abundant ones in rocky habitats. We have not analysed stomach contents of *A. nubila*, but it is likely that it is at rocky shores, like elsewhere, an unspecialized opportunistic feeder, that takes insect larvae as well as plant debris and other items.

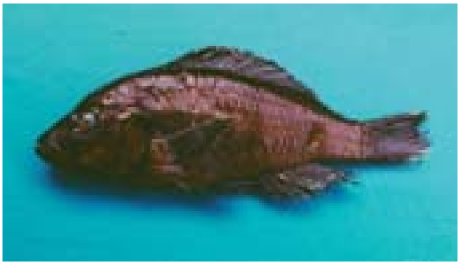
The existence of rock-dwelling populations of this anatomically unspecialized haplochromine, and their coexistence in stable communities with rock-dwelling cichlids of various grades of ecological and anatomical specialization, is a nice example for the apparently paradoxical situation first described by Greenwood (1980) as cladistic gradualism. From an anatomical point of view, an unspecialized insect eater, similar to today's *A. nubila*, could have given rise to the anatomically specialized rock-dwelling *Mbipi*. Some species within the *Mbipi*, such as the epilithic scraper *H. (Xystichromis)* "copper black" and the epilithic picker *H. (Paralabidochromis) chromogynos*, are still fairly close to *A. nubila*, while others such as the epilithic algae scraper *H. (Neochromis) nigricans* and the picker *H. (P.) chilotes* are much more specialized. The puzzling question is, why do species evolve various levels of specialization if others, living alongside with them, perform well without specializing.

Other species with black males, that live in sympatry with *A. nubila* are *H.* ("*A.*") "black cave", *H. (?)* "deepwater", *H. (Xystichromis)* "copper black", *H. (Neochromis)* "velvet black" and *H. (?)* "black pseudonigricans". All differ from *A. nubila* in scale counts, dentition, head shape (table 3), and details of coloration, particularly the latter two differ in anal fin coloration.

***Haplochromis ("Astatotilapia")* "incurved dorsal head profile"** is once again a species with an admittedly unhandy, yet informative, working name. Among all known rock cichlids, this one is anatomically closest to *A. nubila*. It has a somewhat broader lower jaw than has *A. nubila*, and on average more inner tooth rows (table 3). Furthermore the red colour in its fins is much less vivid, the pelvic fins form a less distinct filament, and particularly females have a distinctly incurved dorsal head profile. Its chest scales are large but somewhat deeply embedded. Thus, in several respects, *H. ("A.")* "incurved dorsal head profile" appears like a slightly derived form of *A. nubila*, better adapted to life among rocks. Amazingly, also its number of lateral line pore scales (33) is just slightly above that of *A. nubila*, though already at the lower end of the range of lacustrine haplochromines.

We know *H. ("A.")* "incurved dorsal head profile" only from Igombe Island at the southern Speke Gulf shore. It lives only

A male *Astatotilapia nubila* from Anchor Island.



A male *H*. "black long snout" (Chamagati).

A female *H*. "incurved dorsal head profile"

A male *H*. "incurved dorsal head profile" from Igombe Island.

in shallow immediately inshore waters in gaps between rock boulders and in rockpools, sympatrically with *H. (X.)* "copper black" and *H. (?)* "zebra nyererei" and is less abundant than either of these. Identification of these three sympatric species is in the field sometimes not easy. The coloration of *H. ("A.")* "incurved dorsal head profile" barely differs from that of *H. (X.)* "copper black" but its snout is longer and its lower jaw narrower, though not quite as narrow as that of *H. (?)* "zebra nyererei". Furthermore it differs in dentition and the distinctly incurved dorsal head profile from both other species.

Another species that appears like a slightly modified *A. nubila* with a just slightly increased number of lateral line pore scales (32-33) is ***Haplochromis ("Astatotilapia") "black long snout"***. It is until today known only from Chamagati Island and looks like a dwarf version of *A. nubila*. However, it clearly differs from that species by having bigger and stronger outer teeth that are more strongly recurved and very firmly implanted, with a tendency to procumbent implantation in the lower jaw (somewhat reminiscent of the condition in *Paralabidochromis*); by smaller, deeply embedded chest scales (typical rock cichlid squamation), and by male coloration. The entirely black males lack the red in the anal fin that is typical for *A. nubila* and have less red also in the caudal fin. The dorsal fin has red lappets. The biggest males have a standard length of just slightly above 60 mm. The species inhabits the very gently sloping shore of Chamagati Island in inshore waters of between 0.5 and at least 1.5 m depth, together with insectivorous *Mbipi*, two insectivores of the *Psammochromis* lineage, and *H. ("A.") cf. brownae*. It has a very low population density. In laboratory experiments on feeding behaviour, "black long snout" performed a large variety of feeding techniques. However, it foraged predominantly by "picking", and frequently by "pullscraping", "snapping" and "digging". Thus even this anatomically unspecialized species is able to perform, though probably with low efficiency, pullscraping, the feeding technique that became the most important one among the rock restricted *Aufwuchs*-eaters of the *Mbipi* lineages.

It is a puzzling fact that the two above discussed *nubila*-like species do not only in their outer appearance resemble *A. nubila*, but have also a lateral line scale count that is very close to the condition found

A male *H*. "black cave" from Gana Island. Drawing by Helmut Seehausen.

in riverine *Astatotilapia* (32-33 versus 33-37 in rock-dwelling cichlids of other lineages). The evolutionary significance of this observation is at the moment difficult to assess. However, if the specialized lineages of rock cichlids have evolved from a *nubila*-like ancestor, one could imagine that forms that looked like "incurved dorsal head profile" and "black long snout", stood at the beginning of their radiation. I do not think that these are actually surviving ancestors of the anatomically more derived rock cichlids. It is merely a nice example of the situation that Greenwood (1994) described very aptly by comparing the Lake Victoria cichlid species flock with a car factory, in which prototypes of every model ever produced, and all successive versions of those models are still in production alongside the latest models ("cladistic gradualism", Greenwood 1981, 1994).

Another anatomically generalized species is ***Haplochromis ("Astatotilapia") "black cave"***. It is a small, shallow bodied species that differs slightly from the two above discussed species in several measurements, male coloration and in the number of lateral line scale pores. With 36 such scales it is a typical lacustrine species. Males are black all over with sometimes some golden metallic flush above the pectoral fins, and a dark reddish-brown dorsal head surface and neck. The dorsal fin has red lappets, the caudal fin only the upper and lower corners red, and the anal has a small dull red area in its distal half. The egg dummies are small like in many other rock-dwelling cichlids, and dull yellow. The chest scales are somewhat size reduced but not deeply embedded. We know this species only from deep, dark and cavelike rock pools and crevices among big boulders at steeply sloping islands in the northern Mwanza Gulf, and it seems to be very rare also there.

A completely different species, anatomically quite removed from the *nubila* type by its short head, is ***Haplochromis ("Astatotilapia") brownae*** Greenwood 1962. Greenwood found this species over sand and shingle, where it fed predominantly upon insect larvae (Diptera). Some individuals had eaten many juvenile fishes, and Greenwood sometimes considered this species to be related to certain anatomically little specialized fish eating haplochromines like *H. (Harpagochromis) guiarti* (Greenwood 1962). In rocky habitats we found *H. ("A.") brownae*-like fishes at two places. A not yet further examined population lives at Chamagati Island, and seems to inhabit predominantly areas with small stones and shingle at the very gently sloping small boulder shore. The other population lives at the moderately steep rocky shelf of the main island in the Vesi Archipelago, a purely rocky habitat with medium sized boulders. This population grows bigger than *H. ("A.") brownae* and differs from it by a shorter and relatively broader lower jaw (compare tables 3 and 4).

Males of this ***H. ("A.") "large brownae"*** are light greenish-grey to blueish on the flanks and have light blue lips. The carrot-orange flush on cheek, gill cover, flanks and belly, which is characteristic for reproductively active males of *H. ("A.") brownae*, is but faintly indicated in some males of *H. ("A.")* "large brownae". The dorsal fin is sooty with red lappets, caudal and anal fin are pale red, the latter with pale yellow to orange-yellow egg dummies. The pelvics are black. Both sexes bear six or seven rather broad and irregular vertical bars on the flanks, and particularly females have a short mid lateral stripe, which is most distinct above the anal fin, as is described for *H. ("A.") brownae*. The chest scales are somewhat size reduced and are deeply embedded, like in the majority of rock-dwelling cichlids. *H. ("A.")* "large brownae" lives in waters of between 3 and at least 5 m depth. Of two males that we examined, one had the stomach empty and had insect fragments in its intestine. The other one had only unidentifiable material in stomach and intestine. It is likely that the population of the Vesi rock shelf is a remnant of a once wider distributed species. Remnant populations of several other large predatory species survived at the same place. Witte et al. (1992) found *H. ("A.") brownae*-like fishes over sand in the Mwanza Gulf. Their male coloration was very different from that of the Vesi Island fishes.

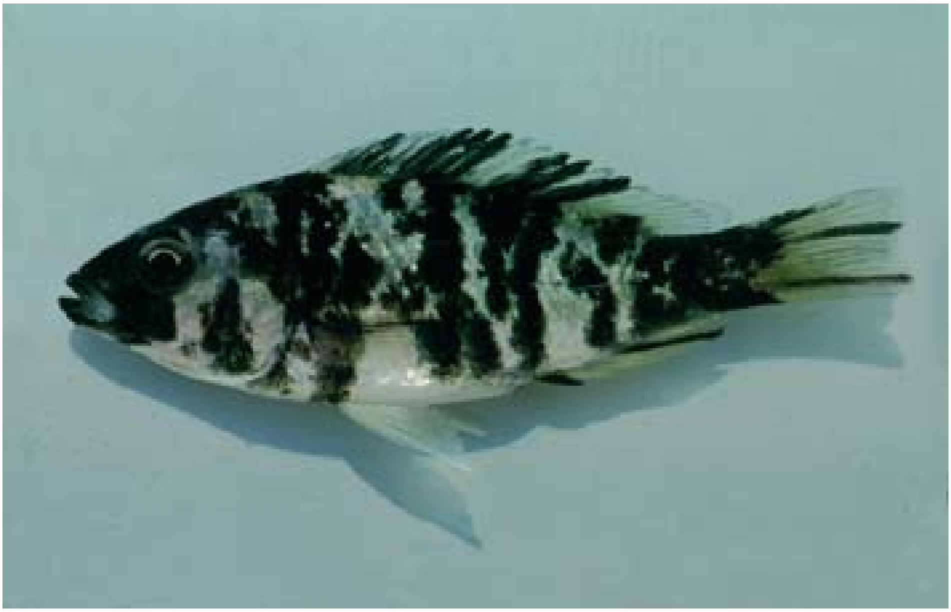
Similar to *H. ("A.") brownae* is ***Haplochromis ("Astatotilapia") barbarae*** Greenwood 1967. It differs from *H. ("A.") brownae* in some morphometric characters (narrower inter orbital width, smaller eye length), fewer gill rakers (8 or 9, *cf.* 9-12), smaller chest scales, and stout bicuspid rather than weakly bicuspid and unicuspid outer teeth (Greenwood 1967). *H. ("A.") barbarae* is a polymorphic species, females of which frequently (or even mostly) are of a piebald morph. The latter exhibits on a silvery-yellow to yellowish ground a variable number of, in shape and dorso-ventral extent irregular blotch-like vertical bars. Less common is the "normal" morph, and rare an OB-morph (Greenwood 1967). Male live coloration is unknown. The melanin pattern is inconspicuous in both sexes, and consists according to Greenwood (1967) of a faint mid lateral stripe, a very faint dorsal lateral stripe (only in females?), and four even fainter vertical bars.

H. ("A.") barbarae is known from the northern, Ugandan waters, and from eastern and southern Tanzanian localities. Like *H. ("A.") brownae*, it lives over sand, shingle and rock (Greenwood 1967, Witte et al. 1992). In the Mwanza Gulf it was found predominantly over rocks (Witte et al. 1992). *H. ("A.") barbarae*, though anatomically rather unspecialized, has a peculiar feeding habit. It seems behaviourally specialized to steel eggs from spawning pairs. Witte-Maas (1981) described in detail how this species feeds on eggs of other rock-dwelling cichlids. In the observed case, a pair of *H. (?) nyererei* was spawning. A female *barbarae* observed the pair from below the water surface at a distance of 60 cm, just outside the range within which the *H. nyererei* male would chase away territorial intruders. Whenever the female *H. nyererei* circled in the nest, the *H. ("A.") barbarae* moved stealthily forward, to withdraw each time that the male circled, who several times chased her away. When the *H. nyererei* female laid some eggs, *H. ("A.") barbarae* rushed forward to snatch the eggs away. This often happened so quickly that the spawning female had not yet even started to collect the eggs. If she was about to do so, *H. ("A.") barbarae* pushed her away. Witte-Maas coined the term "egg-snatching" for this behaviour. She observed that the actions of the egg-snatcher were usually so fast that it managed to disappear from the nest before the male *H. nyererei* could attack it. This strategy was so successful, that the *H. ("A.") barbarae* obtained eggs in 10 out of 11 attempts. Sometimes, however, she attacked while the *H. nyererei* female had not laid any eggs (Witte-Maas 1981).

H. ("A.") barbarae declined dramatically after the Nile perch upsurge and disappeared entirely from its former record localities in the Mwanza Gulf (Witte et al. 1992). We have never seen this species anywhere else either since 1989 (Seehausen et al. in press [b]), nor has it been seen recently at the northern lake shores (Kaufman & Ochumba 1993). If it is not extinct, it is certainly critically endangered. Several haplochromines that have been named *barbarae* by aquarists, belong to different species. Real *H. ("A.") barbarae* have been sent in the early 80s from Uganda to Sweden by B. Selbrink. I do not know what happened to that stock. Those fishes had apparently been caught together with *H. (Paralabidochromis)* "rockkribensis" at a rocky shore.

One of the species erroneously identified as *barbarae*, and which is rather common in the aquarium fish trade, is *Haplochromis (?)* "red piebald" or "piebald redfin". This is a small insect eating species which is caught in the Victoria Nile near Jinja (L. Kaufman pers. comm.). It differs in dentition (tending to *Paralabidochromis* type, unicuspid outer teeth) and coloration from *H. ("A.") barbarae*. The majority of its individuals are orange-blotched (both sexes). The "normal" coloured males have deep blue flanks, a red anal fin, red dorsal fin lappets, and some red distally in the caudal fin. Details about

A male *H.* "large brownae" from Vesi Island.



A female *H. barbarae*, collected and photographed before the Nile perch upsurge.

the ecology of this species are not known.

Insect-eating rock cichlids that cannot be grouped

There are a few insectivorous rock-dwelling haplochromines that I cannot assign to any of the lineages and groups described until here. In some cases this

H. "red piebald" is one of the species erroneously identified as *H. barbarae*. It is a small insect-eating species which is caught in the Victoria Nile near Jinja in Uganda.

A male *H*. "brown narrow snout" from Gana Island.

may be due to their isolated taxonomic position, however, in others it may simply be due to lack of information. Some are now known only from one or two individuals but are anatomically or in terms of coloration so peculiar that I do not want to skip them in this account of rock-dwelling Lake Victoria cichlids. Some have not yet been measured and are hence not represented in table 3.

Three species are anatomically similar and may form a small group on their own but may on the other hand also be members of the Vertical bar *Mbipi*. They are anatomically very close to the "Pseudonigricans" complex of the latter, but differ somewhat in melanin pattern. Their about five broad vertical bars are superimposed by a rather distinct mid lateral stripe that is in one species dissolved into two elongate blotches. The three species occur sympatrically.

A conspicuous appearance with its long, pointed and narrow snout and brown male coloration is ***Haplochromis (?)* "brown narrow snout"**. It is a rare species but apparently has a wide geographical range. We know it from only three localities which are so far apart that the range of the species seems to cover most of the region that we surveyed (see map). Male body and head coloration is brown, sometimes tending to reddish, sometimes with a metallic blue flush on the lower body half. There is a dark mid lateral band. The dorsal fin is dark with orange to red lappets, the dark caudal fin has a narrow orange to red edge. The anal fin is pale reddish in the two northern populations, but yellow in the southern (Hippo Island) population, with orange coloured egg dummies. *H.* "brown narrow snout" is at its record localities rare to very rare. Until today we found three individuals at Hippo Island, two at Mabibi Islands, and five at Gana Island. All but one from Hippo Island were males. The species has everywhere been found at depths between 4 and 7 m. At Hippo and Mabibi the shore slopes moderately steep and the rock boulders are medium sized and big respectively. At Gana the slope is steep and the boulders are very big. All three individuals from Hippo Island (two in 1993, one in 1996) were encountered at the very same spot. This indicates that the species may have particular microhabitat requirements that are not yet understood. Unfortunately nothing more is known yet about the ecology of the fascinating fish.

At Gana Island we recently discovered ***Haplochromis (?)* "pale egg dummy"**. It may have a wider distribution north of our survey area. We found "pale egg dummy" living sympatrically with three similar species at about 4 m water depth among big rock boulders. From "brown narrow snout" it differs by having a less narrow snout, from that species as well as from "orange belly" and "black Ukerewe" ("Pseudonigricans" complex) it differs in male coloration: pale brown with grey fins, the dorsal fin with pale yellowish lappets, the anal fin with big pale yellow egg dummies.

Also ***Haplochromis* (?) "orange belly"** is known only from Gana Island, our northern-most sampling point. It may be more widely distributed at the Ukerewe west coast and north of our survey area. It is of a distinct appearance and differs from "brown narrow snout" and "pale egg dummy" in its finer, acutely pointed and more strongly recurved outer teeth, smaller eyes, and male coloration. The male is on the upper parts of the flanks from the snout to the caudal peduncle pale red. It is bright orange on the gill cover and on the lower half of the anterior flanks between the lateral line and the anal fin insertion, and green on the lower half of the posterior flanks and the caudal peduncle. The dorsal fin is metallic blue with red lappets, caudal and anal fin are red, the pelvic fins black. The mid lateral stripe is dissolved into two broad and elongated blotches. "Orange belly" lives sympatrically with "brown narrow snout" and "pale eggdummy" in the huge rock gardens of Gana Island. We found it in 4-6 m deep water among big boulders.

***Haplochromis* (?) "duck snout"** is a species with a peculiar snout shape that has been discovered in 1995 at the Bwiru Peninsula between the entrances of Mwanza and Speke Gulf, and has not yet been measured. It has large eyes and a rather long snout. The male is light brownish dorsally with a pinkish flush and metallic greenish-yellow flanks, red lappets on the dorsal fin, a red margin to the caudal fin, and a reddish anal fin with orange egg dummies. The female is similarly coloured but lacks the red in the fins. Both have five rather broad vertical bars on the flanks. Nothing is known yet about the ecology of *H.* "duck snout". We collected it in a ca. 1.5 m deep, wide rock pool at a steeply sloping large boulder shore.

***Haplochromis* (?) "blue insectivore"** is probably a member of a *Mbipi* lineage. It is known only from Irondo Point (Sengerema shore) were it lives in very shallow water in strong surf over small rock boulders, sympatrically with *H. (Neochromis)* "velvet black" and *H. (Xystichromis)* "copper black". The male is beautifully metallic light blue all over, with only faint traces of red distally in the unpaired fins. Its coarse unicuspid outer teeth suggest an insect diet. The species has not yet been further investigated.

***Haplochromis (?)* "purple rocker"** is one of the eleven rock-restricted haplochromines that were discovered in 1978 by Frans Witte and Els Witte-Maas at the Nyegezi rocks (Witte et al. 1992). In spite of intensive sampling in that region we failed to find this fish. It cannot be excluded that it declined strongly or went even extinct. Several other species also disappeared from the rocky shores in the north-western Mwanza Gulf (e.g. *H. (Neochromis)* "kruising", *H. (Paralabidochromis)* "rockpicker", and *H. (P.)* "elongate rockpicker").

***Haplochromis (?)* "shovel mouth"** is a peculiar fish of unique appearance of which we caught only one male yet at Igombe Island in a rock pool of 0.5 to 1 m depth. With a combination of a shallow dorsal head profile, a large mouth, and a square shaped lower jaw, this fish is unique within the *Mbipi*. A similar lower jaw shape was previously known only from the oral shelling molluscivore *H. (Hoplotilapia) retrodens* which is otherwise very different from *H.* "shovel mouth".

A male *H*. "pale eggdummy" from Gana Is.

A male *H.* "duck snout" from Bwiru Island.

A male *H*. "orange belly" from Gana Island.

A male *H*. "blue insectivore" from Irondo Point.

A male *H*. "shovel mouth" from Igombe Island.

A territorial male *Haplochromis plagiodon* from a sandy habitat.

A male *H. (Macropleurodus) bicolor*.

Frequent intruders from other habitats

The cichlid communities of rocky reefs and shores are at most places to over 90% composed of stenotopic species, that live only at rocky shores. Most of the remaining species have either rocks and sand (e.g. molluscivores of the *Ptyochromis* lineage), or rocks and submerged vegetation (e.g. algae scrapers of the *Haplochromis* lineage) as their major habitats. However, apart from these two groups of rock-dwellers, one does from time to time encounter haplochromine species in rocky habitats, that are bypassing visitors from other habitats. These "occasional intruders" (Witte et al. 1992) are species the habitats of which are adjacent to rocks, thus littoral sand-dwellers, vegetation-dwellers and, at steeply sloping rock shores, pelagic open water-dwellers. We never found inhabitants of sublittoral mud bottoms, e.g. detritivores, over rocks. Their general absence may be explained by the circumstance that mud bottoms are rarely directly adjacent to rock bottom (at least in the littoral and sublittoral regions of the lake). At the same time soft bottom dwellers are usually more stenotopic with regard to substrate type than are sand and vegetation dwellers. Also among the sand bottom- and vegetation-dwellers some species seem to be less stenotopic and/or more mobile than others, and more often than others intrude into rocky habitats. I briefly introduce these species to the reader.

The species composition among occasional intruders of rocky habitats has changed significantly during the past ten years. This is probably a direct consequence of the Nile perch upsurge. Pelagic, but also sand-dwelling haplochromines were directly affected by the increased predation pressure, and of the 13 occasional intruders that were observed over rocks in the north-western Mwanza Gulf in 1978/79, twelve had disappeared by 1990 (Witte et al. 1992). Except two (*H. (?)* "thick skin", *H. (?)* "kribensis"), none of them has been recorded again over rocks in the Mwanza Gulf between 1991 and 1996. One more (*H. (Macropleurodus) bicolor*) is still occasionally seen over rocks at one place in the Speke Gulf.

Sand-dwelling cichlids are most frequently intruding into rocky habitats, and particularly some oral shelling molluscivores. We observed ***Haplochromis (Paralabidochromis) plagiodon*** Regan & Trewavas, 1928 at a number of steeply sloping rocky islands and rock shores in the Mwanza Gulf, as well as at the very gently sloping Chamagati Island in the Sengerema region. The species is currently one of the most widely distributed haplochromines in southern Lake Victoria, inhabiting exposed sand beaches as well as sublittoral mud bottoms (Seehausen et al. in press [b]). A detailed investigation may reveal a complex of sibling species. Among the rock cichlids only members of the *H. (P.)* "rockkribensis" complex can be confused with *H. (P.) plagiodon*, in particular *H. (P.)* "rock macula" and *H. (P.)* "short snout scraper". *H. (P.) plagiodon* differs from both by having a longer, and less broad lower jaw and a different male coloration (see photos). From "rock macula" it furthermore differs in female coloration. Females of *H. (P.) plagiodon* are brown-grey with narrow and thin vertical bars. From "short snout scraper" it differs also by its less decurved dorsal head profile.

Haplochromis (Macropleurodus) bicolor (Blgr. 1906) disappeared as an occasional intruder of rocky habitats in the Mwanza Gulf, but is still found at one place in the Speke Gulf. According to Greenwood (1956b) it is a widely distributed species, living over sand, rock and shingle but only rarely over mud. It is now almost extinct.

From northern lake shores it has not recently been reported (Kaufman pers. comm.) and the small population in the Speke Gulf is the only one known to still exist in southern Lake Victoria. The last time that I observed some individuals there by Scuba, was early 1996. They joined shoals dominated by *H. (Ptyochromis?)* "red rock sheller" in strongly surf exposed shallow waters over rocks. Possibly the rocks offer them retreat from predation pressure exerted by Nile perch. In coloration the species is not very distinct, though sexually active males in some populations become bright orange or red on the anterior half of the flanks. Piebald (bicolor) morphs do occur. With its strongly decurved dorsal head profile, the unique shape of its upper jaw which curves downwards in the posterior third, and with its unique dentition of stout bicuspid teeth in which the minor cusp is strongly reduced and lies anteriorly of the elongate and buccally orientated major cusp, this species can hardly be confused with any other Lake Victoria haplochromine.

A number of sand-dwelling insect eaters used to intrude into rocky habitats and one still does so. The latter is ***Haplochromis (?)* "thick skin"** (Witte et al. 1992), a beautiful small yellow fish that can be quite abundant at some sand beaches. It seems to be widely distributed since similar fishes have frequently been shipped out from Kenya and Uganda to Europe and America, and are better known among aquarists than many other species. Unfortunately they have in aquarium publications been dealt with under various wrong names. Most often they were mis-identified as *H. obliquidens* and *H. brownae*. Details of the coloration of "thick skin" can vary among populations, but they all have bright yellow flanks with rather many vertical bars. The melanin pattern often resembles that of species of the *H. nyererei* complex. The dorsal fin carries either many red maculae, or is almost entirely red. Often it carries red maculae also in the females. Furthermore do reproductively active males of several populations exhibit an orange to orange-red flush on the gill cover and large parts of the dorsal and ventral aspects of the flanks (see photo). The most diagnostic characters, however, are the peculiar, laterally compressed, tapering mouth, and the long slender bicuspid outer teeth that are much longer than the teeth of the first inner tooth row. *H. (?)* "thick skin" shares with some species of the *Ptyochromis* lineage the habit of "diving" into the sand in case of danger. Riexinger (1996) gives some more information about *H. (?)* "thick skin".

***Haplochromis (?)* "small blue zebra"** is another small insect eater with conspicuous male coloration. Judging from its light pigmentation it is likely to be a sand-dweller. However, it has only a few times been caught both over sand and over rocks in the southern Speke Gulf and central Mwanza Gulf. It was seen for the last time in 1991. This is a tiny species that can hardly be confused with any rock cichlid. It resembles in body shape some other small sand-dwelling insect eaters. Males are light blue-grey with about six regularly shaped vertical bars on the flanks and much red in the unpaired fins (see photo). The coloration of the anal fin is distinct from that in otherwise similar sand-dwelling species. It is almost entirely orange-red to red with two or three rather big egg dummies, surrounded by broad transparent rings.

A very little known insect eater is ***Haplochromis (?)* "blue and orange fins"** that is sometimes found over rocks at the southern Speke Gulf shore. We have not found its real habitat yet, but its large, not deeply embedded chest scales, combined with its being very irregularly caught, suggest that it is not a real rock-dwelling species.

After sand-dwellers the second most common intruders of rocky habitats are species that normally live among submerged vegetation (e.g. in water-lily and *Ceratophyllum* beds), near emerging vegetation (reed, papyrus) or under floating

A male *H*. "thick skin" from Nyegezi Bay.

A male *H.* "small blue zebra" from Nyegezi Island.

Above: a freshly caught *Haplochromis* "blue and orange fins" from Ndurwa Bay.

Right: a female Haplochromis "macula" from Nansio Bay. The author frequently found it over the rock formations of piers.

A male *H*. "macula" from Nansio Bay.

vegetation (water hyacinths, reed, papyrus). Though submerged vegetation is inhabited by many species of insect eating and algae scraping haplochromines, we encountered of them only algae scrapers in rocky areas. This may reflect the way how these species reach rocky areas. In many cases they are likely to arrive with islands of floating reed, papyrus, and water hyacinths. Insect eating species are much less abundant than algae scrapers in the vicinity of such vegetation. They are more common in submerged vegetation.

***Haplochromis (Haplochromis)* "macula"** is a brilliantly coloured algae scraper with a tooth shape that suggests it to be a member of the *Haplochromis* lineage. It used to be abundant in littoral areas of the northern Mwanza Gulf before the Nile perch upsurge and was found also slightly offshore over sand and mud bottoms (Witte et al. 1992). After the Nile perch upsurge it disappeared from the offshore parts of its habitat range but continued to be found inshore in the vicinity of reed and papyrus. We frequently found it over the rock formations of piers. Recently we discovered a population that inhabits shallow water of a rocky island in the northern Speke Gulf. It lives at a place where litter from overhanging large trees accumulates on the rock bottom, and possibly constitutes a food source for this species. Its high abundance at that place suggests that it is there a real rock-dweller, rather than an occasional intruder of the rocky habitat. Males have a bright red head, chest, belly, and dorsal aspects of the flank. The remainder of flanks and caudal peduncle are yellowish-greenish. The dorsal fin is red in the spinous part and transparent with red streaks and maculae in the soft part. The caudal fin is blue-grey with red maculae in the upper half, and the anal fin is pale whitish with two or three big orange or orange-yellow egg-dummies. Females and quiescent males frequently exhibit an elongate dark blotch on the flanks above the anal fin which is part of an otherwise very faint, broken mid lateral stripe. Hence the name "macula". However, I have not seen this blotch in the fishes from the northern Speke Gulf. With this blotch, the melanin pattern of *H. (H.)* "macula" differs somewhat from that of other species of the *Haplochromis* lineage (see page 230).

***Haplochromis (Haplochromis)* "black and red fins"** is another epiphythic algae scraper with a *Haplochromis* type dentition. It resembles in size and head shape *H. (H.)* "purple yellow" but has a different dentition, with more slender, often obliquely truncated outer teeth, and fewer inner tooth rows. We found it in the vicinity of floating *Eichhornia* over rocks at Makobe Island. We know only males yet. They are black with red lappets to the dorsal fin, a red caudal fin margin, and an entirely red anal fin that carries yellow egg dummies. The latter are unusually small for a species of the *Haplochromis* lineage.

Witte et al. (1992) list five pelagic and half pelagic plankton eating haplochromines that used to intrude into rocky habitats from the open waters. Four of them have not been seen after 1987, neither in their major habitats in the open water, nor at rocky shores. They are possibly extinct (Witte et al. 1992, Seehausen et al. in press [b]). The phytoplankton eater ***Haplochromis (?)* "kribensis"** (Witte et al. 1992) is very occasionally still seen at rocky islands in the northern Mwanza Gulf. Early in 1996 we discovered a remnant population at a rocky island in the northern Speke Gulf. It is the only known place where *H. (?)* "kribensis" is not only occasionally encountered but was, at least during our visit, quite abundant. While scuba diving I observed *H. (?)* "kribensis" in mixed shoals with *H. (H.)* "macula" in the upper 1 m of the rocky littoral. Possibly it should here not be considered an occasional intruder but rather a rock-dweller. This exceptional situation may be explained with the above mentioned unusual character of the rocky habitat at this place: litter from overhanging large trees accumulates on the rock bottom, and may form directly or indirectly an additional food source for species that are not normally rock-dwellers.

The coloration of male *H. (?)* "kribensis" is reminiscent of that in *H. (Paralabidochromis)* "rockkribensis". However, "kribensis" males are less yellow and have a silvery iridescent area on each scale, giving them a silvery ("pelagic") appearance. The light silvery females differ distinctly from the deep yellow "rockkribensis" females. The melanin pattern of "kribensis" consists of, in their width irregular vertical bars and broken mid and dorsal lateral stripes, while "rockkribensis" has a typical chessboard pattern. *H. (?)* "kribensis" is the only representative of the ecological group of phytoplankton eating cichlids, that is still encountered in southern Lake Victoria. In the time before the Nile perch upsurge, it used to inhabit the surface layers of sublittoral waters (Witte et al. 1992). During the past five years it has much more often been seen in rocky littorals than in open water. The protection of its remnant populations should be given high conservation priority. ***Haplochromis (?)* "citrus"** is another phytoplankton eater that used to be seen occasionally over rocks, but it seems to be extinct (Witte et al. 1992).

In the pre-Nile perch era four pelagic or half pelagic zooplankton eaters had been recorded over rocks (Witte et al. 1992). For one of them (*H. (?) thereuterion*) rock bottom was the major habitat, and a recent study showed that it was mores insectivorous than planktivorous. I discussed this species in another chapter. Three others were occasional intruders. Neither the surface dwelling ***Haplochromis (?)* "argens"**, nor the more bottom orientated ***H. ("Astatotilapia") megalops*** Greenwood & Gee, 1969 and ***H. ("Astatotilapia") piceatus*** Greenwood & Gee, 1969 have been seen after 1987 anywhere in the lake. They are possibly extinct (Witte et al. 1992).

Witte et al. (1992) finally listed five species of fish eaters as occasional intruders in rocky habitats in the northern Mwanza Gulf. Four of them, ***H. (Prognathochromis) macrognathus***, ***H. (Prognathochromis) perrieri***, ***H. (?)* "big teeth"** and ***H. (?)* "longurius"** seem to be extinct in the region, and have not been reported from other parts of the lake either (Kaufman & Ochumba 1993, Kaufman & Seehausen 1995). Of the fifth species, ***H. ("Astatotilapia")* "two stripe yellow green"**, we found in 1991 one individual in a beach seine, pulled over sand bottom. After 1991 it has also not been seen any more. In 1989 we caught a juvenile ***H. (Harpagochromis) altigenis*** Regan, 1922 over rocks at Anchor Island in the northern Mwanza Gulf. That was the last sighting also of this large predator.

A male *H*. "kribensis" from Kilimo Island.

A female *H*. "kribensis" from Nansio Bay.

A female H. "argens".

A male *H*. "argens" in the aquarium.

A male *H. piceatus* in the aquarium.

H. cf altigenis from Anchor Island.

H. "yellow insectivore", another 'golden' haplochromine from lake Victoria.

A courting male *Astatoreochromis alluaudi* in the aquarium.

Astatoreochromis, Oreochromis and Tilapia at rocky shores

Eight cichlid species that are not part of the Victorian species flock, live alongside with the several hundred species of the haplochromine flock in Lake Victoria. Apart from *Astatotilapia nubila* that is treated in another chapter, these are the haplochromines *Astatoreochromis alluaudi* and *Pseudocrenilabrus multicolor victoriae*, four species of *Oreochromis* and one or two species of *Tilapia*.

Pseudocrenilabrus inhabits marginal swamps and creeks and we never found it at rocky shores. ***Astatoreochromis alluaudi*** Pellegrin 1903, though found in marginal waters as well, is a common inhabitant of truly lacustrine environments and is found at most rocky shores and islands. It is easily identified by its golden yellow coloration that is particularly intense on the underside, and by its high count of anal fin spines (4-6 *cf.* 3 in the species of the haplochromine species flock and *Astatotilapia nubila*). Further peculiarities are a rounded caudal fin (*cf.* a truncate or subtruncate one in members of the flock) a high number of egg-dummies arranged in up to four rows on the anal fin of the male, and otherwise very muted differences in coloration of male and female. Based mainly on these characters, Greenwood (1959b, 1979) considered *A. alluaudi* distinct from the members of the species flock of Lake Victoria. This was confirmed later by biochemical work (Sage et al. 1984, Meyer et al. 1990). To avoid misidentifications, it should be said here that meanwhile several *Haplochromis* species are known from Lake Victoria that also have many egg-dummies (see photos under *H. (Paralabidochromis)* "rockkribensis" complex) and at least one other species with golden male coloration, resembling that of *A. alluaudi*.

A. alluaudi lives now predominantly at rocky shores and among or in the vicinity of submerged and emerging vegetation. Before the Nile perch became abundant in Lake Victoria, *A. alluaudi* inhabited also sublittoral mud bottoms (Witte et al. 1992). It is not any longer found in such habitats. At many rocky shores it constitutes a frequent member of the community. Even far offshore islands, such as the purely rocky Ruti and Mabibi Islands, and the Vesi Archipelago in the Speke Gulf have their *A. alluaudi* populations. We found unusual anal fin coloration among males of these populations at the geographically isolated central Speke Gulf islands. Males at all places that I have visited along the mainland shores of Lake Victoria, including the northern, Ugandan shore, as well as at less far offshore islands, have a largely red anal fin. Males from Ruti Island frequently have entirely yellow anal fins, and at the Vesi Archipelago as well as at Mabibi Islands a form with a distinctly white anal fin lives alongside the normal form with a red fin. These cases of aberrant coloration in populations of *A. alluaudi* at geographically isolated rocky islands may indicate that migration and therefore gene flow between such populations and the inshore main population is limited.

A. alluaudi in Lake Victoria feeds predominantly on snails of the hard shelled species *Melanoides tuberculata* (Greenwood 1959b) which it crushes between hypertrophied pharyngeal jaws, equipped with molariform teeth. Over rock bottoms it frequently coexists with other pharyngeal crushing haplochromines. Usually some spatial segregation can be observed among them, *A. alluaudi* inhabiting the shallower, the other species the deeper parts of the habitat. It is interesting that this non-endemic, eurytopic, but trophically specialized haplochromine species is quite successful in species rich communities of stenotopic rock cichlids.

Of the tilapiine cichlids found in Lake Victoria, only *Oreochromis (Nyasalapia) variabilis* and *O. (Oreochromis) esculentus* are native to the lake. The others have been introduced. Most of these introductions have been done in the 1950s and early 1960s (Oguto-Ohwayo 1990). Already before that, the stocks of the two native species had been declining considerably due to overfishing. The introduced species are now much more abundant, and much more widely distributed in the lake than the natives. In the following I give a short account of the role of the tilapiine cichlid species at rocky shores. For identification and more detailed information, the reader is referred to Trewavas (1983) and Witte and Van Densen (1996).

The Nile tilapia, ***Oreochromis (Oreochromis) niloticus*** (Linnaeus. 1758), was probably introduced to compensate the decline in stocks of endemic tilapiines. It became that much abundant in Lake Victoria that it is now, together with the Nile perch and the "lake sardine" (a cyprinid), dominating the commercial fish catch. Its juveniles and subadults are common at rocky shores and may locally even dominate the fish communities numerically. The larger subadults of between 10 and 20 cm standard length are the main target of many fishermen at rocky shores. I have observed large shoals of juvenile *O. niloticus* grazing from rocks in shallow waters. Particularly subadults mix with various species of rock-dwelling haplochromines. By Scuba diving I found spawning arenas of this species at the foot of rocky reefs, along the rock-sand border at 6-8 m water depth. Males construct rather deep spawning pits of about one metre in diameter and can turn the rock-sand interface into a crater landscape. Simply nothing is yet known about the impact of the Nile tilapia on haplochromine rock cichlids. It is likely that, with its high population density, it exerts competitive pressure upon some haplochromines.

Oreochromis (Oreochromis) leucostictus (Trewavas 1933) was probably introduced accidentally together with *O. niloticus* (Ogutu-Ohwayo 1990). It is less abundant and more restricted to inshore areas with shallow water. At rocky shores it can locally be quite numerous. I have observed reproductively active territorial males in shallow water in the vicinity of reed growing among littoral rocks. These territorial males are very beautifully deep black with white spots on body and fins, and red eyes. They occupy territories of several square metres diameter, from which they keep other tilapiines, but also larger haplochromines away. They are quite aggressive and seem to dominate over the males even of the biggest haplochromines that utilize the same habitat (e.g. *H. (Neochromis) nigricans*, *H. (N.)* "giant scraper").

Tilapia (Coptodon) zillii (Gervais 1848), and probably ***T. (C.) rendalli*** (Blgr. 1896), was or were introduced to convert macrophytes into commercially exploitable food fish. These plant eaters are at rocky shores less common than the two above discussed microphagous species, and are probably merely occasional intruders from habitats with submerged vegetation. In those habitats *Tilapia* species are likely to compete with plant eating haplochromines. However, again very little is known about any possible interaction.

Native to Lake Victoria is ***Oreochromis (Nyasalapia) variabilis*** (Blgr.) 1906. Known in parts of the lake region as *Mbiru*, it is the only representative of the tasselled "Tilapias" (subgenus *Nyasalapia*) in the Lake Victoria basin. Before man introduced *O. variabilis* into a number of ponds in eastern Africa, its geographical distribution was restricted to Lake Victoria, the Victoria Nile above the Murchison Falls, Lakes Kyoga, Kwania and Salisbury, and the lower reaches of the Kagera and Orangi rivers, both draining into Lake Victoria (Trewavas 1983). In Lake Victoria this was originally the dominant tilapiine species at rocky shores. Its young feed upon the algae growth on rocks in shallow water. Adults feed predominantly on loose bottom algae, mostly diatoms, and to lesser extents on phytoplankton (Fryer 1961, Fish 1955, Lowe-McConnell 1956). To spawn, adult fishes move into shallow areas with sandy bottoms and construct nests. These are of a particular architecture,

A fry-guarding female *Oreochromis variabilis*.

A male *Oreochromis variabilis* at Makobe Island.

An OB morph of *Oreochromis variabilis*.

A male *Oreochromis niloticus* from Zue Island.

Tilapia rendalli from Mashoro Bay.

Oreochromis esculentus from a satellite lake near the Mwanza Gulf (Ziwawa Wanawake).

Oreochromis leucostictus from Makobe Island.

a shallow saucer of 13-25 cm in diameter, with an about 2 cm high raised rim, surrounded by a circle of small pits, which is the centre of a larger pit of 30-90 cm diameter (Trewavas 1983).

The population of *Oreochromis variabilis* in Lake Victoria declined dramatically during the last decades. The species is now extinct in large parts of its former range. In the late 1970s it was still frequently encountered at rocky shores in the northern Mwanza Gulf (F. Witte pers. comm.). In spite of intensive search, we could not trace any individual during our rock shore survey. We found *O. variabilis* only at one offshore island in the Speke Gulf (Makobe Island). At that island we observed the species over several years and it appears that a small, but possibly viable remnant population exists.

The reasons for the decline of *O. variabilis* are not well understood. Competition with introduced species of tilapiine cichlids seems to play a role in it. While the two native species *O. variabilis* and *O. esculentus* were ecologically segregated and did not compete much (Fryer 1961, Ogutu-Ohwayo 1990), the habitat demands of the introduced *T. zillii/rendalli* and *O. leucostictus* are similar to those of *O. variabilis* (Ogutu-Ohwayo 1990, pers. obs.). Fryer (1961) described that young *T. zillii* compete for food with young *O. variabilis* and aggressively dominate over the latter. I observed at Makobe Island large habitat overlap between *O. variabilis* and *O. leucostictus* of all size classes. In mixed groups of young fish *O. variabilis* were far outnumbered by *O. leucostictus*. However, while adult males of the latter have their territories in shallow, immediately inshore waters, reproductively active males of *O. variabilis* are found somewhat further offshore. Competition with *O. niloticus* is also probable. Subadults of the latter are abundant in shallow inshore waters, overlapping with both other species. Adult males construct their big spawning pits at 6-8 m depth. Apart from competition with introduced species, increased predation pressure by man and Nile perch may play a role in the decline of *O. variabilis*.

Adult *O. variabilis* can be distinguished from those of the other tilapiine cichlids in Lake Victoria by bright orange to red dorsal fin lappets. Juveniles lose their tilapia-mark (a dark blotch on the dorsal fin at the border between spinous and rayed part of the fin) earlier than those of other species (at a standard length of about 1.5 cm). Subadults can be confused with those of *O. leucostictus* but have more (31-32 *cf.* 28-31 according to Trewavas; 30-33 *cf.* 28-30 according to Hest/Tafiri & FAO/Danida) lateral line pore scales. A peculiarity of *O. variabilis* is its polychromatism. Apart from the "normal" blueish to greenish-grey morph a very beautiful orange blotched (OB) morph, a rarer piebald, and a very rare white morph are known. These brightly coloured morphs, known as *Maradadi*, are more frequent among females, but occur also among males (Trewavas 1983). Their coloration is similar to respective morphs among haplochromine cichlids.

The second native tilapiine cichlid of Lake Victoria, ***Oreochromis (Oreochromis) esculentus*** (Graham 1928) has probably never been more than just a bypassing visitor at rocky shores. It used to live further offshore than *O. variabilis*, and usually over soft muddy bottoms. It is closely related to *O. niloticus*, from which it was geographically isolated before the latter species was introduced into Lake Victoria. Overfished since the beginning of our century, *O. esculentus* has been strongly declining in Lake Victoria (Ogutu-Ohwayo 1990) and is now extinct in the largest part of the lake. The introduction of its larger growing relative, *O. niloticus*, may have sped up this process through competition and/or hybridization. In the late 1980s we encountered occasionally a juvenile of this species at rocky shores in the northern Mwanza Gulf. In the 1990s we never saw any. The photograph shows an individual from a remnant population surviving in a satellite lake near Mwanza.

Non-cichlid fishes from rocky shores

Though the fish communities of rocky shores, reefs and islands in Lake Victoria are dominated by cichlids in species numbers and individual numbers, a good number of other fish species occur in these habitats. Several of them occupy specific ecological niches, in which they dominate over cichlids. Examples are the surf zone-dwelling *Garra*, the cave-dwelling, nocturnal predatory catfish *Bagrus docmac*, and the reef edge-dwelling, predatory Nile perch. Many of these species directly or indirectly interact with cichlids and therefore should be considered in any attempt to improve understanding of the ecology and evolution of rock-dwelling cichlids. Nile perch and *Bagrus* are important cichlid predators. Small and juvenile *Barbus* and "lake sardines" are food for fish eating cichlids, but may at the same time compete with zooplankton eating cichlids for food. *Garra* and *Labeo* may compete with *Aufwuchs* eating cichlids for food, and catfishes of the genus *Synodontis* may compete for food with snail eating cichlids. A detailed discussion of such interactions is beyond the scope of this book. Nevertheless, I would like to at least mention and show in a few photographs the most frequently encountered non-cichlids of rocky shores.

At least 44 species of non-cichlid fishes have so far been recorded from Lake Victoria (Hest/Tafiri & FAO/Danida). Of these we recorded 19 at rocky shores in our survey area. Probably only one or two of them are restricted to rock habitats, but in the life history of several others rocks play an important role, and for some they may be the most important places of retreat from the high predation pressure in more open habitats. Thus rocky habitats may be important for the survival of some not habitat restricted species of non-cichlids.

Six species of cyprinids live over rock bottom. *Garra dembeensis* is restricted to this substrate. We found it only at fully surf exposed shores and also there only in the uppermost littoral zone between the surface and maximum one metre depth. It is most frequently seen over horizontal and diagonal rock surfaces at depth of merely a few decimetres. *Garra dembeensis* is a very mobile algae scraper, mostly seen while busy rasping off algae from the rocks. Anatomically it is, with a very shallow, cylindrical body and a subterminal mouth, equipped with a sucking disk, highly specialized for algae scraping in shallow, heavily moved water. It seems to utilize a niche that none of the algae scraping cichlids is utilizing. It is interesting that in Lake Malawi (Nyasa), where *Garra* does not occur, rock-dwelling cichlids (*Labeotropheus*) have adapted to fill the niche of the surf zone algae scraper. *Garra dembeensis* has a wide geographical distribution in central African rivers, reaching as far west as Cameroun.

Anatomically similar to *Garra* are the much bigger *Labeo* species (often commonly called African carps), of which one, *Labeo victorianus* lives in Lake Victoria, and is currently found almost exclusively over rocky substrate. This is a beautiful yellow species which is endemic to Lake Victoria and probably closely related to the central African *Labeo weeksii*. *Labeo victorianus*, at the lake known as *Ningu*, is a migrator that ascends into rivers to spawn during the rainy season (Cadwalladr 1965). Introduction of modern gillnets, set at the river mouths during migration, caused a strong decline of this species since the 1950s, and the collapse of a once commercially important fishery. However, the species is surviving at low population densities. Islands with extensive rocky shelves that have medium sized rock boulders in deeper waters (be-

Barbus tripleurospilus.

Labeo victorianus at Mashoro Bay.

yond 5 m depth), are currently probably the most important habitat of half-grown and adult *Labeo* in the lake. In former days the species used to live predominantly over muddy bottoms (Kudhongania & Cordone 1974). In the rocky areas *Labeo* probably feeds upon epilithic algae and debris.

The only large growing barb of Lake Victoria, the endemic *Barbus altianalis*

Barbus kerstenii from Bukoba.

Bagrus docmac from Python Island.

radcliffi, at the lake known as *Kuyu*, has dramatically declined as well, and is now considerably more rare than *Labeo*. Different from the latter, it used to prefer hard, sandy and stony bottoms rather than mud. We found it very occasionally at gently sloping rocky shores and islands in shallow water (not beyond 4 m depth). It feeds predominantly upon insect larvae, crustaceans and molluscs (Balirwa 1984).

Like *Labeo* it migrates upstream into rivers to spawn and has been strongly overfished. Two small barbels, *Barbus jacksonii* and *Barbus kerstenii* are encountered in sheltered inlets at rocky shores. The first species more frequently than the latter. Both feed on zooplankton and small benthic invertebrates. Finally the "lake sardine", in East Africa known as *Dagaa* or *Omena* (*Rastrineobola argentea*) is a regular visitor of rocky habitats. It is a small "sardine like" shoaling cyprinid that feeds on zooplankton in the pelagic zone of Lake Victoria. Shoals can frequently be observed at rocky shores, particularly where steeply sloping rocky peninsulas penetrate into the sublittoral pelagic zone. Contrary to most other species, this one strongly increased concomitantly with the Nile perch upsurge and haplochromine decline (Oguto-Ohwayo 1990, Wanink 1991), and forms now an important pelagic fishery. Over rocky bottom, it is sometimes hunted by fish eating haplochromines (van Oijen 1992).

Two other, largely pelagic, zooplankton eating fishes that frequently live over rocks, are the alestides (formerly characides) *Brycinus jacksoni* and *Brycinus sadleri*, locally known as *Nsoga*. They are particularly frequently observed in sheltered places, where rocky habitats are surrounded by extensive shallow waters, e.g. in the southern Mwanza Gulf. Such areas are relatively poor in planktivorous rock cichlids. The two species are fairly similar in habitus. However, *B. jacksoni* is a representative of the large growing African alestides and has large scales, reminiscent of the central African *B. macrolepidotus*. *B. sadleri* remains much smaller and has smaller, less prominent scales. We found them frequently in sympatry. The cyprinodonts (killis) *Aplocheilichthys pumilus* and *Aplocheilichthys loati* are two tiny and strictly littoral zooplankton feeders, that can be observed at somewhat sheltered inlets, where some reed grows among the rocks. I saw them moving around rather "respectless" above the heads of haplochromines. *A. pumilus* stays a few decimetres below the surface, *A. loati* is a strict surface-dweller.

Elephant-snout fishes (Mormyridae), at the lake known as *Domo-domo* or *Mbete* (Ukerewe region), were probably once more common at rocky shores than they are today. Seven species have been recorded in Lake Victoria of which three are endemic. All have strongly declined in recent years. The only species that we repeatedly observed in rocky habitats is *Mormyrus kannume*, a large growing species that is widely distributed in the drainage system of the Nile. When found over rocks, it is usually over medium sized boulders, and slopes that are not too steep. Just one time we caught a *Marcusenius sp.* over rocks. Two endemic species, *M. rheni* and *M. victoriae* live in the lake. Mormyrids feed in the rocky zone probably on insect larvae.

Three groups of piscivorous non-cichlid fishes play a role in the fish communities over rocky bottom: Spiny eels, bagrid and clariid catfishes, and Nile perch. Spiny eels (Mastacembelidae), which are quite speciose at Lake Tanganyika rock shores, are, in Lake Victoria, represented by only a single species: *Caecomastacembelus frenatus*. This is a very beautiful one, dark brown with a net of light irregular lines on the head, a light dorsum and a light brown reticulated underside. Little is known about its ecology. We caught it at rocky islands in the Mwanza Gulf and I met it a few times while diving at Makobe Island in the Speke Gulf. It lives in crevices among small and medium sized rocks and is usually seen only half, the head and anterior body standing out while the rest remains hidden among the rocks.

At least five catfishes live over rocks, among them the two *Synodontis* species endemic to the Lake Victoria basin. Both have strongly declined after the Nile perch upsurge (Goudswaard & Witte in press) and are generally rarely seen. We observed the bigger *S. victoriae*, locally known as *Gogogo*, somewhat more often over rocks than *S. afrofisheri* (*Ngere*) which we found just two or three times. Both species feed on snails and insect larvae. Six species of clariid catfishes, locally known as *Mumi* or *Kambale*, are known from Lake Victoria, two of them endemic. We regularly encountered two species in rocky habitats. One is probably the small *Clarias liocephalus*, the other one is still unidentified but is probably the juveniles of *C. gariepinus* or another large growing species. Both live in crevices among rocks. Possibly they prey upon small fishes. We never found adults of *C. gariepinus* among rocks. The most common catfish in rocky habitats is *Bagrus docmak*, locally known as *Hongwe*. *Hongwe* and Nile perch are probably the most important fish eating predators in rocky habitats apart from birds and spotted neck otters. We found *Bagrus* in all size classes, though full adults were rarely caught by our gears. *Bagrus* hunt probably by night. During day light they hide in crevices among the rocks and as a diver one can see hardly more than their long antennas peeping out from crevices. Small individuals are usually found in shallow waters, bigger ones stay deeper.

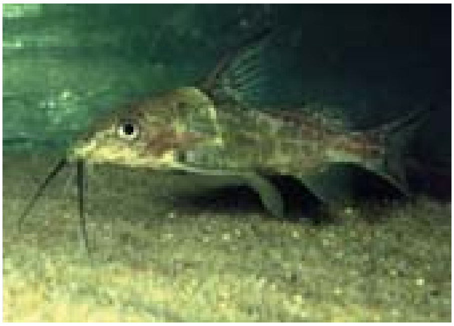
Last not least, also the top predator of the changed ecosystem of Lake Victoria, the Nile perch (*Lates sp.*), locally known as *Sangara* lives in rocky habitats. In the past it was believed that Nile perch would not live among rocks (Witte et al. 1992). However, sampling of various rocky shores and islands, and particularly scuba diving at these, has in the meantime learned us that this generalization is not (or not any more) correct. Nile perch is quite a frequent member of the rock-dwelling fish communities. However, its abundance differs between localities, and not at all places does it invade the shallow waters. It appears that Nile perch in rocky habitats of the Mwanza Gulf are smaller and invade shallower water than those at offshore islands in the Speke Gulf and in the open lake. The size range of 31 Nile perch, caught in January 1996 over rocks at three islands in the southern Mwanza Gulf, was 10 to 40 cm standard length (mean 16 cm). Stomach content analysis of such rock-dwelling Nile perch revealed that individuals of 15 cm standard length can swallow adult rock cichlids of 7 cm standard length! The adult haplochromines found in Nile perch stomachs at Python Islands and Makobe Island were *Haplochromis nyererei* of both sexes. Apart from preying upon haplochromines, rock-dwelling Nile perch prey on the larvae of dragon flies (Odonata) and on prawns (*Caridina nilotica*).

At the offshore islands in the Speke Gulf that are surrounded by deep water, catch frequencies of Nile perch in shallow inshore parts of the rocky habitat are low, but I regularly observed larger Nile perches, of between 40 and 60 cm standard length, in deeper waters. They seemed to patrol the rocky reefs at between 6 and 15 m water depth as if hunting haplochromines. However, haplochromines seemed not to pay very much attention to the predators. I met exceptionally many large and very deep bodied Nile perches at 6 to 7 m depth at the very steep slope of the offshore Miandere Islands east of Kome Island/ Sengerema region. Lying on the ground or slowly moving along it, I had continuously between two and four of them in my sight which was restricted by water transparency to a radius of about 3 m. These Nile perches were rather homogeneous in size and were almost certainly targeting at rock-dwelling haplochromines. The way they patrolled the steep slope without being much scared by a diver, was reminiscent of sharks patrolling a coral reef. These scuba observations confirm reports of fishermen that they have discovered places with large Nile perches at rocky shores in the Sengerema region (D. Chitamwebwa pers. comm.)

Mormyrus kanume from Makobe Island.

A subadult *Lates sp*. at Kissenda island.

Synodontis victoriae.



Synodontis afrofisheri.

Evolution of rock-dwelling cichlids

Most discussions about the evolution of the cichlid species flock of Lake Victoria had been imprinted by the case of the endemic species of Ugandan Lake Nabugabo (e.g. Fryer & Iles 1972, Greenwood 1980, 1994). Lake Nabugabo is a small satellite lake of Lake Victoria. It was a lagoon of the latter until a drop in water level separated it from the main lake about 4000 years ago. Populations of five haplochromine species that got in Nabugabo isolated from the main lake populations, evolved into new endemic species (Greenwood 1965). The short time that was sufficient for these populations to speciate, suggested that the mechanism of speciation in satellite lakes could be suitable to explain a major part of the explosive speciation of Victorian cichlids (Greenwood 1980). However, as discussed in the chapter on the history of the lake, that mechanism alone, appears unsuitable to explain the radiation of the cichlid species flock. Distribution patterns among and ecological characters of the lithophilic cichlids provide evidence against the satellite lake hypothesis, and for other mechanisms of speciation (Seehausen 1996b, below). This does not mean that the process of speciation in satellite lakes does not take place. It certainly exists, and may have played a role also in the explosive multiplication of species, but it is most unlikely that it was the only, or the most important process. Instead of discussing the shortcomings of the satellite lake hypothesis, I want to make an attempt to construct from several lines of circumstantial evidence an integrated hypothetical picture of events and processes, that may have been of importance in the evolution of rock-dwelling cichlids in Lake Victoria.

The distribution of melanin patterns and patterns of chest squamation, as well as similarities in the not yet decoded "general appearance" of rock-dwelling cichlids, suggest that the majority of these are derived from only two different ancestral species (diphyletic origin). At least the larger one of the two major groups, the Vertical bar *Mbipi*, is anatomically and in their feeding modes diverse, but is known exclusively from rocky habitats. This implies that their ancestor first evolved its specificity to this habitat, before it underwent radiation into different feeding niches within the rocky habitat. For the second group, the Chessboard *Mbipi*, the evidence for their primary radiation in rocky habitats is less unambiguous, since several species have been found also in other habitats.

Evolution of habitat specificity and trophic primary radiation

When a lacustrine habitat began to develop by back-ponding of rivers (see the chapter on the history of Lake Victoria), the riverine ancestor of the modern lake cichlids must have been confronted with a major new and vacant adaptive niche, the open water body. A response to this situation, that has been documented in several groups of bony fish, is the splitting of the gene pool of the formerly riverine and now lacustrine species into a benthic (littoral- and bottom-dwelling) and a limnetic (open water-dwelling) species (Bentzen & McPhail 1984, Bentzen et al. 1984, Skúlason et al. 1989, Taylor & Bentzen 1993, Taylor & McPhail 1994). A splitting into these two adaptive types may have been the first speciation event in the cichlid population during the riverine-lacustrine transitional period in the early days of Lake Victoria. As the lake increased in size, habitat diversity also increased, and the benthic species may have split up further into forms that inhabited the major substrate types. By adaptation to the different habitats in behaviour and/or coloration, hence by changes that incidentally affected the Specific Mate Recognition System (SMRS, see the chapter on taxonomy), reproductive isolation between these forms may have evolved. Similar events seem to still happen among the modern cichlids of Lake Victoria (see under *H. (?) tanaos* and *H. (?) thereuterion*). By that time distances among patches of rocky substrate must have been relatively small and the shallow open water separating them was no formidable barrier to migration. Similar situations exist at present in the shallow southern parts of the Mwanza Gulf, where each rock-dwelling species seems to form one outbreeding population, and we found little, if any intraspecific geographical variation. Thus, it is likely that the species that got adapted to the conditions in rocky habitats, made up one large population with frequent migration between rocky habitat patches.

The dominance of Vertical bar *Mbipi* in species and individual numbers, as well as in ecological diversity in any rock cichlid community of modern Lake Victoria, suggests that it was their ancestor that first colonized the rocky habitat in this early phase. After it got behaviourally and anatomically adapted to the rocky habitat, and as habitat diversity continued to increase, this ancestral rock-dwelling species may have undergone trophic radiation. Again, in analogy to what is now known from other bony fish, the result of this trophic primary radiation

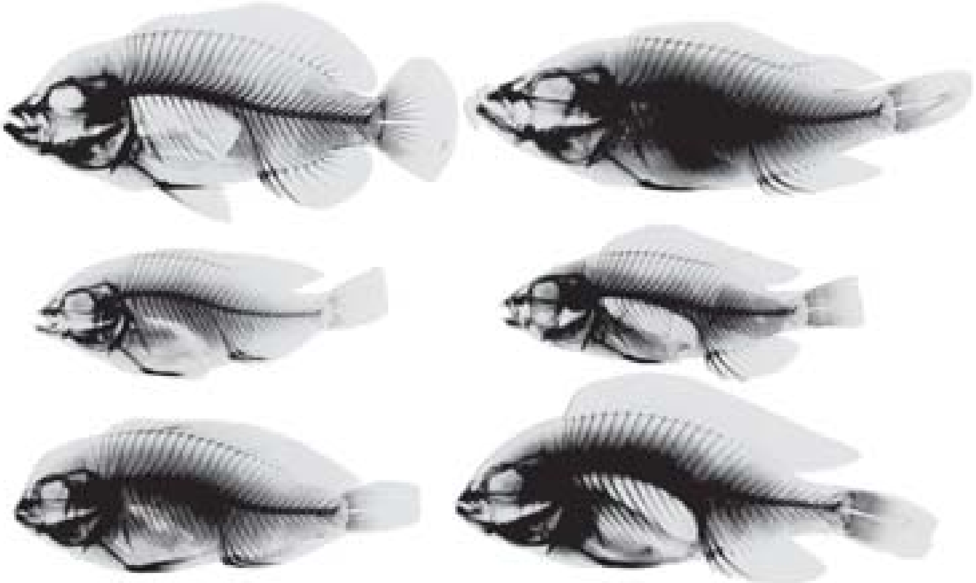


Figure10a: Examples of anatomical diversity of rock-dwelling haplochromines (X-ray photographs): *(a)* Major adaptive types within the Vertical bar *Mbipi* (left column) and Chess-board *Mbipi* (right column) as the result of trophic radiations within both lineages.
Upper row: Species with a long head, moderate to relatively long lower jaws, and relatively small eyes feed predominantly on larger insect larvae (e.g. Ephemeroptera) but also on plankton. *H. (?)* "deepwater" ("Deepwater" complex, left). *H. (Paralabidochromis) chilotes* (*Chilotes* complex).
Middle row: Species with a short head, short lower jaws, and large eyes feed predominantly on small insect larvae (e.g. Chironomidae). *H. (?)* "black and yellow pseudonigricans" ("Pseudonigricans" complex, left). *H. (Paralabidochromis)* "Zue rockpicker" ("Rockpicker" complex).
Bottom row: Species with a steep dorsal head profile and short but broad and strong lower jaws predominantly scrape algae from the rocks. *H. (Neochromis) nigricans* (*Neochromis* complex, left), *H. (Paralabidochromis)* "short snout scraper" ("Rockkribensis" complex).

may have been more benthically and more pelagically feeding species. As compared to the ancestral species, the benthic foragers increased their biting power by developing short jaws, supported by strong muscles to scrape unicellular and/or filamentous algae from the rocks, the others increased their sucking efficiency by developing longer jaws and a protrusile mouth to prey upon insect larvae and/or plankton (text figure 11a). Such could have been the origin of the major species complexes of vertical bar *Mbipi* (*Neochromis*, *Xystichromis*, *Nyererei* complex, "Deepwater" complex, "Pseudonigricans" complex). Though all of them exhibit some diversity in feeding modes and anatomy, the different modern lineages are on average clearly adapted to different feeding modes. That these modes are complementary in the sense of trophic niche partitioning is apparent from the structure and composition of modern rock cichlid communities (Seehausen et al. in press [a], Seehausen & Bouton 1996a, see chapter on ecology).

A role for sympatric speciation?

This trophic primary radiation is unlikely to have happened by allopatric speciation. It does not appear plausible that the descendants of an ancestral population, if

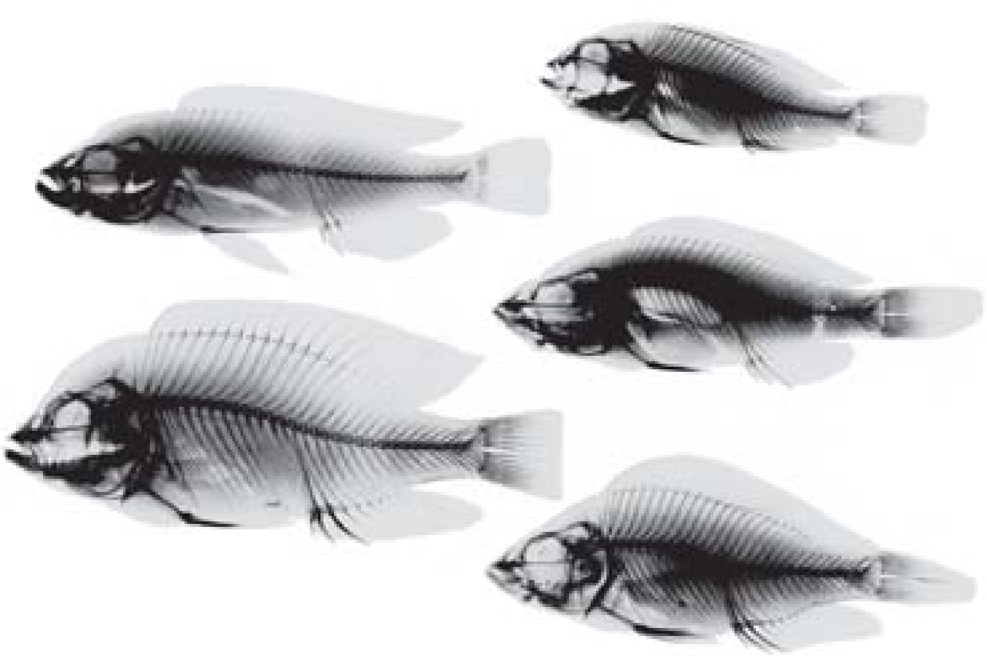


Figure 10b: adaptive types of other rock-dwelling lineages:
Upper right: Snail shellers have a steep dorsal head profile, short but strong jaws, and very procumbently implanted teeth (*H. (Ptyochromis) sauvagei*).
Upper left: Paedophages have a short head, relatively long and very strong lower jaws (*H. (Lipochromis)* “velvet black crypotodon”).
Middle right: Fish and crab eaters have a long head and long lower jaws (*H. (Harpagochromis) howesi*).
Lower left: Snail crushers are deep bodied and have strongly enlarged pharyngeal bones (*H. (Labrochromis)* “stone”).
Lower right: Predators of large insect larvae and small molluscs have a longer head and slightly enlarged pharyngeal bones (*H. (Psammochromis) saxicola*).

X-ra

An example of polychromatism: different morphs of *H*. "blue scraper" at Makobe Island.

An example of a sympatric sibling species pair: two series of males of *H*. "red pseudonigricans" and *H*. "blue pseudonigricans" caught in a single haul.

split over several lake basins, would in each basin evolve specificity to rock substrate, but evolve in each basin a different mode of feeding, and that these feeding adaptations are complementary to each other. Moreover, that rock-cichlid communities in Lake Victoria comprise the same species complexes at all until now sampled places would not be explained. The possibility of speciation in the absence of geographical barriers (sympatric speciation) has always been disputed. However, recent evidence from molecular genetical studies makes likely that sympatric speciation in fish, including African cichlids, is happening (Taylor & Bentzen 1993, Schliewen et al. 1994, Taylor & McPhail 1994). In all these cases, the speciation events coincided with the invasion of a riverine species into a vacant lacustrine environment, and with a splitting into more benthic and more pelagic feeders.

Some circumstantial evidence from rock-dwelling cichlids suggests that Lake Victoria cichlids are able to speciate in the same way. We found several cases of almost identical geographical distribution of two anatomically very similar species (sibling species), that differed slightly in microdistribution and feeding, and distinctly in male coloration. Their distribution patterns do not give any evidence for that they may have speciated in allopatry. These sibling species pairs usually consist of one species that feeds more benthically and one that feeds more pelagically. Examples are "blue" and "red" "pseudonigricans", "blue" and "yellow" "deepwater", and "zebra" and "red" *Nyererei*.

According to the basic model of sympatric speciation (Maynard Smith 1966), speciation in the absence of geographical isolation is possible if (1) morphs of a polymorphic species have different selective advantages in different microhabitats, (2) display some differences in microhabitat distribution, and (3) mate assortatively. It is most likely that the frequent occurrence of polymorphism in Victorian rock cichlids is instrumental in sympatric speciation. Polymorphisms are most apparent if they concern male nuptial coloration (male nuptial polychromatism). However, polymorphisms in

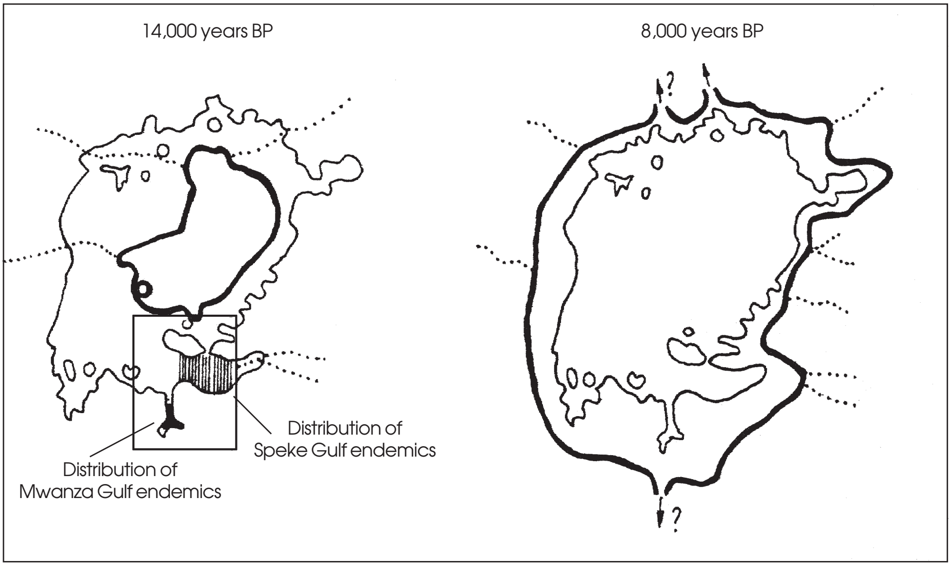


Figure 11. Two major areas of endemism in relation to pre-historic lake level fluctuations. Thin line = boundaries of present days Lake Victoria. Bold line = boundaries of the pre-historic lake (after Stager et al. 1986). Further explanation in the text.

jaw anatomy and dentition exist as well among rock cichlids (see page 79). Particularly differences in anatomy are likely to cause differential advantages in different microhabitats with different food sources. When an anatomical polymorphism gets genetically linked with a male polychromatism, the conditions for sympatric speciation may be fulfilled. In that case, morphs may evolve into reproductively isolated species.

If sympatric speciation via polymorphism exists among the modern Lake Victoria cichlids, it may have played an important role in the trophic primary radiation of the rock cichlids. By the time of this assumed trophic primary radiation of rock-dwelling cichlids the lake may still have been small and migration between rocky areas likely caused a spreading of the new feeding types, each represented by one species, over the entire lake.

The more the entire Victorian species flock became diversified, the more different lineages would have happened to invade the rocky habitat. However, they met with already well adapted Vertical bar *Mbipi* and could establish themselves only here and there, where vacancies existed in the *Mbipi* communities (text figure 11b). For instance the *Ptyochromis* lineage successfully occupied the niche of the oral shelling snail eater at rocky shores. Apart from the Vertical bar *Mbipi* only one lineage (the Chessboard *Mbipi*) underwent a real secondary radiation that must at least partly (*Paralabidochromis* "rockpicker" complex) have happened in the rocky habitat. This lineage may have been pre-adapted to fill vacancies in the communities of Vertical bar *Mbipi*, because of their quite different jaw anatomy. Alternatively, if nascent Lake Victoria still consisted of more than one lake basin by the time that habitat specificity had evolved, the two melanin pattern lineages among the rock cichlids may have had their origins in two different basins. However, the distribution all around the lake of one or two species of most feeding types of both melanin pattern groups, implies that a single basin had already formed before the secondary radiations began.

Secondary radiations by allopatric speciation

As the lake continued to grow, the waters separating patches of rocky habitat became deeper, distances between them larger. This may have led to a restriction of gene flow among the populations of rock-dwelling cichlids. The dwindling chances of an emigrant to reach another patch of rocky habitat would have reinforced habitat specificity. As a consequence of their increasing geographical isolation, populations likely started to diverge from each other. Today this situation can be observed among populations of rock-dwelling cichlids in the northern Mwanza Gulf. Allopatric populations of several species that live at patches of rocky habitat, separated by sublittoral areas of 10-15 m depth, differ in anatomy (N. Bouton, J. de Visser, C.D.N. Barel & O. Seehausen in manuscript), coloration (see page 276) and genetics (Dorit 1990). Where gene flow was little enough, differences evolving among allopatric populations likely affected the SMRS. Individuals of such different populations when they happened to meet again, would not have recognized each other any more, but behaved as two different species. Distribution patterns suggestive of this kind of allopatric speciation can be observed within complexes of sibling species in the Speke Gulf, where distances among populations are bigger, and the waters separating them deeper than in the Mwanza Gulf (e.g. "blue nyererei"/"pink anal"/"red rim anal", "blue scraper"/"velvet black"). In this way rapid multiplication of each adaptive type, originally represented by one species, is likely to have happened (secondary radiation) as stasimorphic speciation (speciation without major anatomical innovation) in intralacustrine allopatry.

There are several lines of evidence for that intralacustrine speciation was common among rock-dwelling cichlids:

(1) *Regional endemism and lake basin*

history. During a period of dry climate, about 14,000 years BP, the water level of Lake Victoria was about 70 m lower than it is now (Stager et al. 1986, see the chapter about the history of the lake). If the lake had not completely dried up by then, it was considerably smaller than it is now. The part of the lake, the cichlid fauna of which is described in this book, was entirely dry (see text figure 12). A large number of rock-dwelling cichlid species is now endemic to parts of this relatively recently re-flooded area. These species almost certainly have evolved after the lake had come back, thus within the last 13,000 years. Moreover, 8000 years ago the lake level was much higher than it is now (see text figure 12). Flat rocky islands, like Makobe Island in the Speke Gulf must have been flooded that deeply, that stenotopic shallow water-dwelling rock cichlids like *Neochromis* would not have found suitable conditions. The Mwanza Gulf, as a peripheral arm of the lake, did not exist because the lake shores were a good distance further south. It is likely that its endemic species, and many endemics of other southern regions evolved within the past 8000 years. Interesting in this respect may be a major water level recession that has been dated back to about 3700 years BP (Temple 1967).

(2) *Chain species.* If deep water is a barrier to gene flow among populations of rock-dwelling cichlids, gene flow should occur predominantly along the mainland shores and along underwater ridges. If in this way restricted gene flow leads to speciation within the lake, one would expect chain species to occur. Chain species consist of a series of geographically isolated populations, the first and the last of which behave as reproductively isolated species when they happen to meet, though they are connected by intermediate populations, among which gene flow exists. An example of what looks much like a chain species is provided in text figure 13.

Factors driving divergent evolution in allopatry

If gene flow between allopatric populations is little, differences between populations can arise merely by incidence. However, circumstantial evidence suggests that several factors may accelerate genetical changes in allopatric populations. Partial correlations between male coloration and characters of the light regime in the specific environment of a cichlid population strongly suggest that light regimes have an impact on the evolution of coloration (see pages 121ff and 138ff). Since coloration in turn is likely an important component of the SMRS, populations that have been living under different light conditions (deep *versus* shallow waters, steep *versus* gentle slopes, clear *versus* murky waters, among *versus* above rock boulders etc.) sufficiently long enough to evolve genetical adaptations, are likely to be reproductively isolated upon secondary contact. Examples might be the blue and the red coloured "Short snout scrapers" (page 163ff), and the blue and black "Pseudonigricans" complex species (pages 133 and 135). Such cases of sibling species differ from those suggestive of sympatric speciation in that the distributions of siblings are in large mutually exclusive, and areas of overlap are marginal to their geographical ranges. Further evidence for the impact of light regimes on male coloration is the recurrent appearance of coloration patterns in different groups living under similar ecological conditions, and therefore under similar light regimes. Examples are black males with yellow fins in the *Nyererei* and "Pseudonigricans" complexes, and males with a red dorsum and blueish underside in the same two species complexes.

Many species of rock-dwelling haplochromines exhibit polymorphisms in male nuptial coloration (Seehausen & Bouton 1996, further examples in this book). While possibly playing a role in sympatric speciation, these polychromatisms may also have an accelerating impact on the process of allopatric speciation. They may often pro-

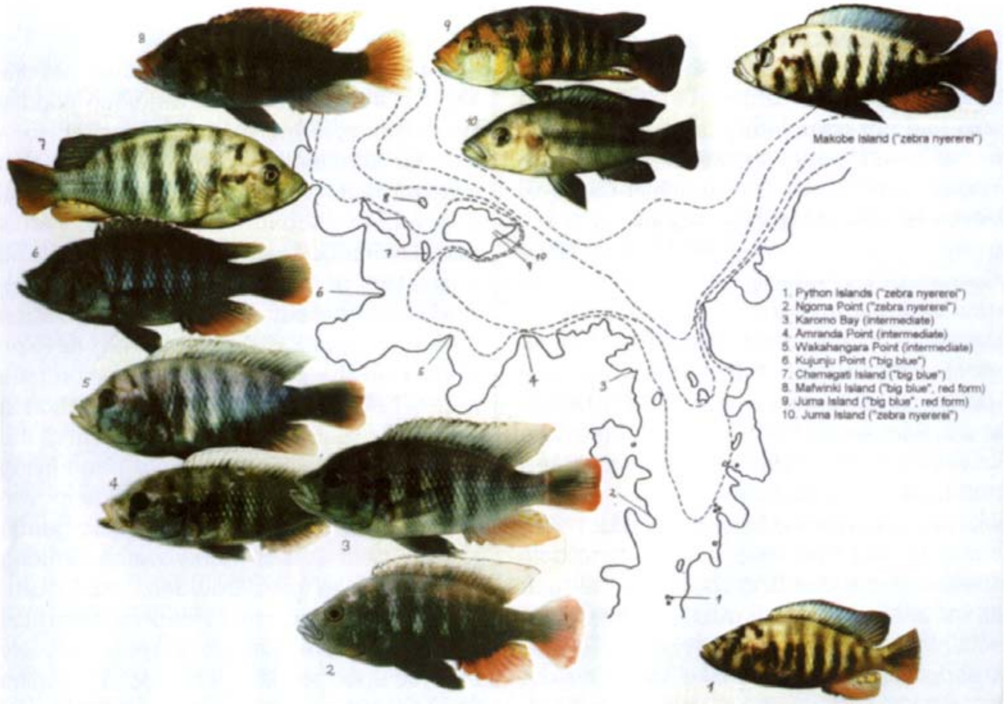


Figure 12: Distribution patterns among *H.* "zebra nyererei", *H.* "big blue", and intermediate populations, suggestive of a chain species complex. At Juma Island both species live sympatrically.

vide the material upon which selection will act. A good example are the red and yellow anal fin morphs of *H. (?)* "yellow chin pseudonigricans" (page 138). Selective advantages of the one or the other morph under different light conditions will, over sufficiently long time, lead to the extermination of the second morph. Probably the most important selective advantage of a male colour morph over another one is a higher attraction for females. In haplochromine cichlids females are usually the sex that chooses the partner (Dominey 1984, Seehausen 1996b). Thus, the more attractive male colour morph leaves on average a higher number of offspring. Hence its relative abundance will increase on cost of the less attractive morph. Speciation by such sexual selection is completed, once the alternative colour morphs are eliminated from two populations, together with the respective female recognition criterion. This may have happened in *H. (?)* "black and yellow pseudonigricans" and *H. (?)* "blue pseudonigricans" that, compared to the widely distributed *H. (?)* "yellow chin pseudonigricans", lost the red anal and the yellow anal fin morph respectively (pages 133 and 135).

Interaction among species, may potentially play a major role in the process of allopatric speciation by sexual selection. For instance interspecific competition for territorial space or for food, may cause the individuals of a population to diverge from their "usual" microhabitat, and to expose themselves to aberrant light regimes (see the discussion under *H. (?)* "blue nyererei"). The females' mate choice would then do the rest. It is probably the same polymorphisms that are instrumental in allopatric and sympatric speciation under different situations, and it is likely that both mechanisms of speciation played a role in the secondary radiations of rock-restricted cichlids, though the number of sibling species pairs that exhibit distribution patterns suggestive of allopatric speciation is bigger.

Matrix species

Possibly as a consequence of the above sketched temporal sequence of events, almost every rocky shore cichlid community in modern Lake Victoria is composed of the same basic faunal elements: *Neochromis*, *Xystichromis*, *Nyererei* complex, "Pseudonigricans" complex and "Deepwater" complex (the latter two can be missing in particular habitat situations) of the Vertical bar *Mbipi*, "Rockkribensis" complex, "Rockpicker" complex, and *Chilotes* complex of the Chessboard *Mbipi*. Moreover, each of these complexes comprises one species or superspecies that is distributed throughout the investigated parts of the lake, and a much larger number (except in the *Chilotes* complex) of regional endemics. I refer to the widely distributed species as to the *matrix species** [foot note: *my use of the term *matrix species* is slightly different from the use by Kaufman (in press)] of each lineage. I propose the following explanation of this distribution pattern: By the time the lake started to grow bigger, and rock-dwelling populations got geographically isolated from each other, each feeding type, represented by one species (the ancestor of each modern species complex) was distributed all around the lake. As gene flow among populations decreased, some populations may have undergone genetic changes faster than others (due to small population size and/or strong local selection regimes) and may have had changed their SMRS by the time that a new wave of immigrants of the matrix species reached their habitat patch. Such populations would not crossbreed with the matrix species, but would persist next to it as a second species.

Due to the wide distribution of the matrix species, the probability that it colonizes each rocky habitat patch repeatedly is very high. The probability that it re-colonizes a patch inhabited by a new species is bigger than the probability that a new species spreads to other patches. Therefore, it is unlikely that a matrix species got extinct from any place forever, as long as migration was not entirely disrupted. At the same time, it takes long for a localized new species to spread. If in this way, the large and widely dispersed ancestral form of each species complex has been carried along until today in form of the matrix species, while butting off regional daughter species, the distribution patterns found among the modern *Mbipi* species would largely be explained. At present it is difficult to test the hypotheses proposed here because molecular genetics do not yet reveal enough variation among Lake Victoria haplochromines to resolve the phylogenetic puzzle. However, with the further improvement of techniques and the development of new ones, I am optimistic that this will become possible.

Lates sp. with and adult male *H. nyererei* in its stomach. In front a second *H. nyererei* of similar size for comparison.

Conservation of rock-dwelling cichlids

After the loss of large parts of the cichlid fauna of Lake Victoria, following the boom of the Nile perch (*Lates sp.*, Witte et al. 1992), rocky habitats became a major refugium for cichlid species diversity. Rocky habitats currently harbour the most species rich, and the ecologically most complex fish communities (Seehausen et al. in press [b]). This has been attributed to the absence of Nile perch from such habitats. Recent investigations by use of Scuba, however, revealed that Nile perch is quite abundant and quite able to hunt in rocky habitats. It seems that the spatial complexity of the habitat allows cichlid populations to withstand the predation pressure, and that the balance between predator and prey is being maintained better than in other habitats.

Most of the cichlid species that are now living at rocky shores are stenotopic rock-restricted species like the *Mbipi*. Several others, however, were more widely distributed in the pre-Nile perch era, but survived in the Nile perch era only at rocks. Most, if not all of these "rock refugees" have already in the pre-Nile perch era occurred in rocky habitats, while many similar species, that have not occurred in such habitats, went extinct. Thus, the cichlid species assemblage that survived the Nile perch boom in rocky refugia, is not a random sample, but rather a selection of pre-adapted species. Nevertheless, it is ecologically diverse, and includes species such as the fish eaters *H. (Harpagochromis) cavifrons* and *H. (Harpagochromis) serranus*, the paedophages *H. (Lipochromis) cryptodon* and *H. (Lipochromis) melanopterus*, the insect eater *H. (Paralabidochromis) chromogynos*, the pelagic phytoplankton eater *H. (?)* "kribensis", and the tilapiine *Oreochromis variabilis*. The characters, that make these species pre-adapted to inhabit rocky substrates, may differ among species.

Despite the importance of rocky habitats as the most species rich cichlid refugium, species diversity is declining there as well. Regrettably, in the pre-Nile perch era, rocky shores have been studied only in a very small area (northern Mwanza Gulf: Nyegezi Rocks, Kilimo Island, Anchor Island, Hippo Island). From this area at least eight rock-dwelling haplochromines (*H. (Neochromis)* "kruising", *H. (?)* "purple rocker", *H. (Paralabidochromis)* "rockpicker", *H. (P.)* "elongate rockpicker", *H. (Harpagochromis) howesi*, *H. (H.) guiarti*, *H. ("Astatotilapia") barbarae*, *H. (Lipochromis) melanopterus*) and many occasional intruders disappeared until 1996. This is about one third of the original rock-dwelling fauna of the area. During the past five years we witnessed population declines of several other species. The abundance of *H. (?)* "zebra nyererei" at Python Islands decreased by the factor four between 1991 and 1995 (Seehausen et al. 1996). *H. (Neochromis) nigricans* at the same islands declined even stronger (Seehausen 1996c). *H. (Paralabidochromis)* "rock macula" may have gone extinct at Nyegezi Rocks between 1993 and 1996 (see page 167).

Several factors seem to contribute to the decline of rock-dwelling cichlids. Lake Victoria is undergoing eutrophication at an increasing rate (see the chapter on limnology). As a consequence of eutrophication a considerable decrease in water transparency is observed. This is likely to affect cichlid communities via its impact on food resources and on the reproduction system. Most if not all haplochromine species of Lake Victoria produce viable and fertile offspring if they happen to hybridize. As a consequence of this reproductive compatibility, reproductive isolation among species is labile. If prezygotic reproduction barriers break down, nothing will prevent hybridization, by which two species may become one. While many haplochromines that inhabit murky waters over sublittoral mud bottoms, are seasonal spawners and have distinct spawning areas (Goldschmidt & Witte 1990), many rock-restricted species spawn throughout the year, and their spawning sites are largely identical with their foraging sites (Seehausen 1996d and unpubl. data). Segregation of species by spawning area or spawning season can therefore not play a major role in maintaining reproductive isolation among them, but specific mate recognition (see the chapters on taxonomy and evolution) must be of particular importance. If male coloration plays an important role in mate recognition, reproductive isolation can break down if decreasing transparency of the water goes with changes in the aquatic light regimes. Such changes are usually a narrowing of the light spectrum, and a relative loss of short wave lengths. As a consequence, colour signals can be set out of function which may lead to hybridization among otherwise similar species. Patterns suggestive of such or similar events have been described (Seehausen 1996b) and are corroborated by strong correlations between species richness and aquatic light regimes (Seehausen, J.J.M. van Alphen and F. Witte unpubl. data).

Fishing pressure at rocky shores and at many islands has increased considerably over the past decade. In some regions fishermen target at rock-dwelling haplochromines for human consumption. Almost everywhere they are collected in large numbers as the most important bait in Nile perch long line fishery. At many places, finally, they are a common by-catch of tilapia fishermen. The tilapia fishery with line and large hooks affects predominantly the larger haplochromines. Particularly deleterious, however, is the use of poison (insecticides) for fishing. This has become a rather common practice of fishermen targeting at *Oreochromis niloticus* at rocky shores. Cichlid communities at very small rocky outcrops can be heavily affected by poison. It is likely that frequent poisoning leads to changes in species composition: stenotopic species with low dispersal abilities, thus most local endemics, disappear, while widely distributed species with higher dispersal abilities take over (Seehausen et al. in press [b]). Generally, the small population sizes typical for many rock-dwelling cichlids, make them particularly vulnerable to fishing.

The water hyacinth (*Eichhornia crassipes*) is a floating weed that originates from South America, but has spread over large parts of Africa. It is present in Lake Victoria since the 1980s and underwent in southern Lake Victoria recently rapid expansion (Bwathondi & Mahika 1996, Seehausen et al. 1996). It now covers large areas in sheltered situations like the Mwanza Gulf. Its impact on the cichlids at rocky shores is considerable. Weed carpets deprive the rocky littoral of light, cause water stagnation, rapid accumulation of rotting plant material among the rocks, and, consequently, oxygen depletion. Fish densities under permanent weed carpets are low, and rock-restricted cichlids decline in favour of more eurytopic species like *H. (Haplochromis)* "purple yellow". These changes in species composition can be observed even under the relatively light water hyacinth carpets of unstable extension, that are found in exposed situations. At places where the water transparency allowed Scuba observations, I observed that *Mbipi* species like the epilithic algae scrapers of the *Neochromis* lineage, and pickers of the *Paralabidochromis* lineage, are among the first species to disappear under water hyacinths (Seehausen et al. 1996). Strongly affected are furthermore those species that live in rockpools and rocky crevices in shallow water (e.g. *H. (?)* "zebra nyererei"). Their habitat can be entirely destroyed when the interstices among the rocks are getting filled up with rotting plant material.

Eutrophication, overfishing, and spreading of water hyacinth all have negative impacts on the cichlid species diversity at rocky shores. Nile perch predation may have its impact as well, as may have competition with rock-dwelling stages of the introduced tilapiine cichlids (see page

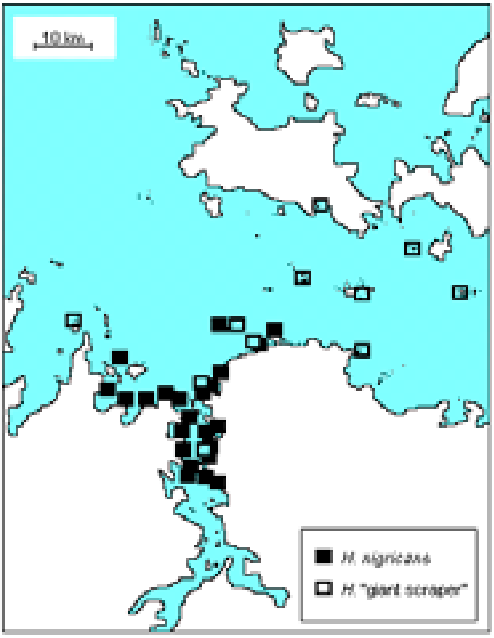
The load of sediments and nutrients flushed int the lake by rivers has increased tremendously because of deforestation.

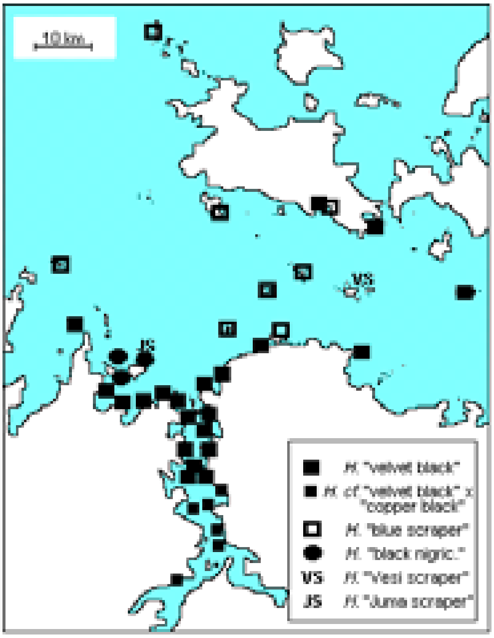
258ff). Regrettably, little attention has been paid in the past to the fish communities of rocky shores in Lake Victoria. Hence we are just beginning to understand their importance in the ecosystem and the factors threatening them. A conservation strategy to protect these communities is urgently needed. However, as many of the threats are problems that affect the ecosystem in its entirety, conservation strategies can only be successful, if incorporated in a larger management plan for the Lake Victoria basin.

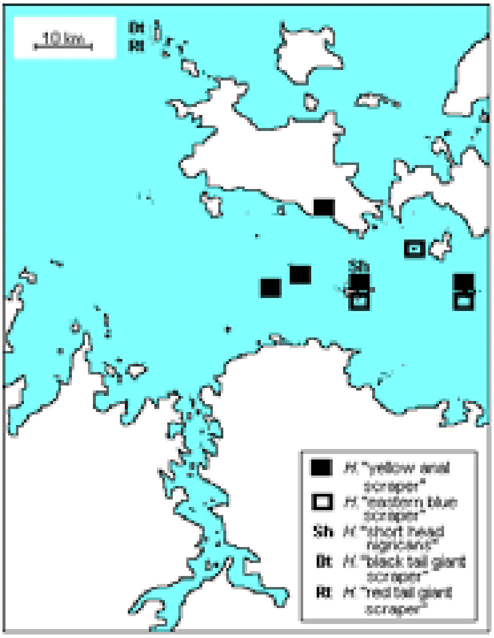
The most urgent need is to provide the industries and towns around the lake with efficient waste water treatment systems to slow down water pollution and eutrophication. More than 40 industrial plants operate, and seven large towns are situated along the lake shores. According to Tanzanian news sources, over two million litres of untreated sewage and industrial waste are discharged into the lake every day. If this situation is not changed, we will very soon be left with mere remembrance and fragmentary knowledge of a once extraordinarily rich species diversity at rocky shores.

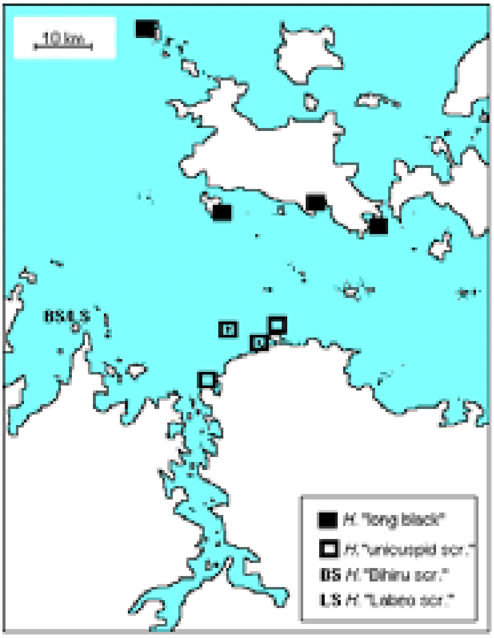
Some of the threats to the rocky shore fish communities are topographically localized, and the establishment of fish parks would be useful to protect at least some areas against them (e.g. overfishing). To choose appropriate sites for park establishment, the taxonomical and ecological inventory of species diversity along rocky shores has to be continued, and should encompass the shores all along the lake. Unfortunately it is at present very difficult to secure the financial means that are needed to implement such tasks. Finally, the upcoming aquarium fish trade with rock-dwelling Lake Victoria cichlids should consider the small population sizes of many of its target species. If it is well organized and implemented, aquarium fish export may help to create locally and globally awareness of the values that are at risk. However, if not, it may as well pose one more threat to the survival of rock-dwelling cichlids in Lake Victoria.

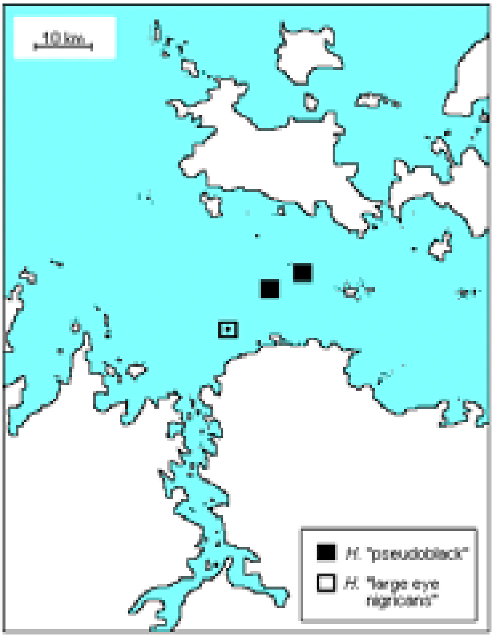
Distribution maps

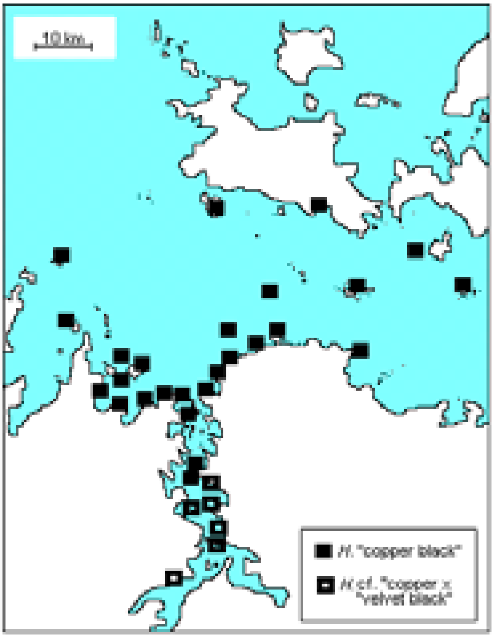


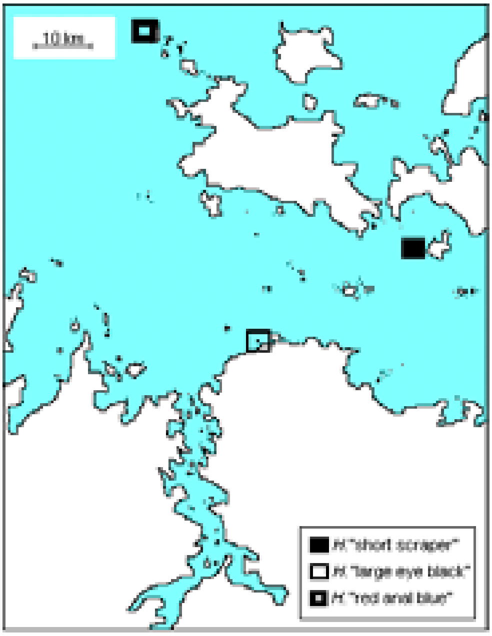


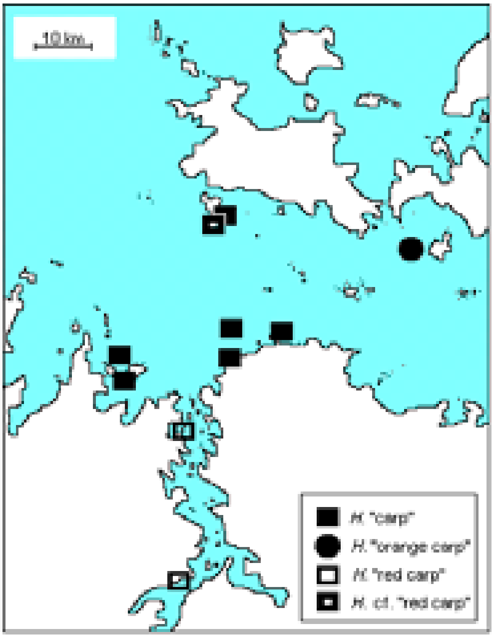


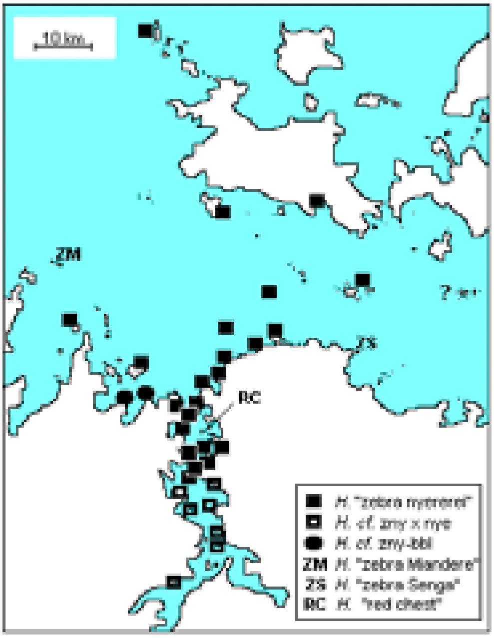


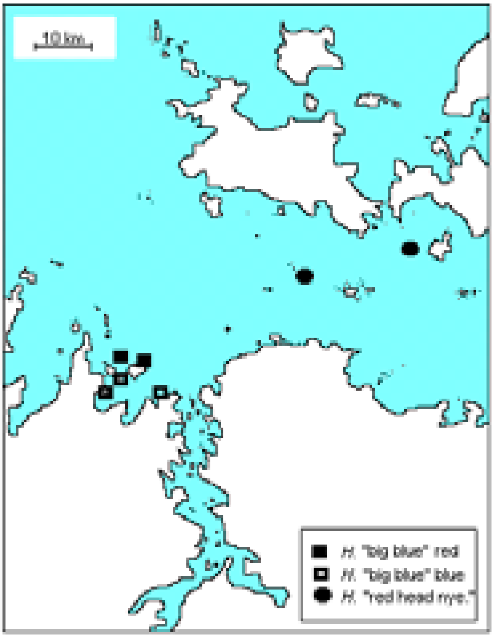

10 km
■ H. "pseudoblack"
☐ H. "large eye nigricans"

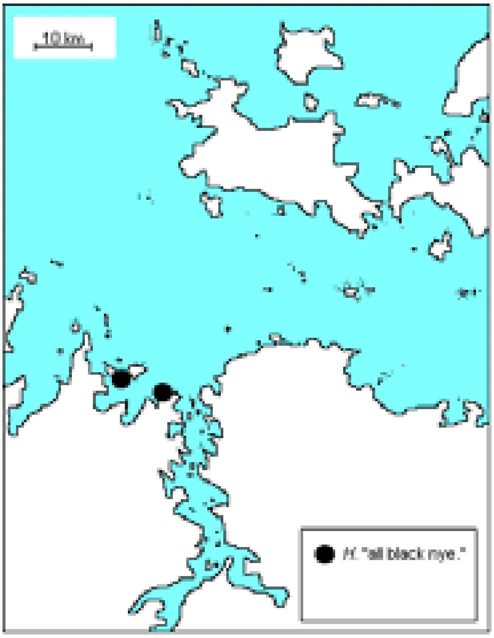

10 km
■ H. "copper black"
▣ H. cf. "copper x "velvet black"

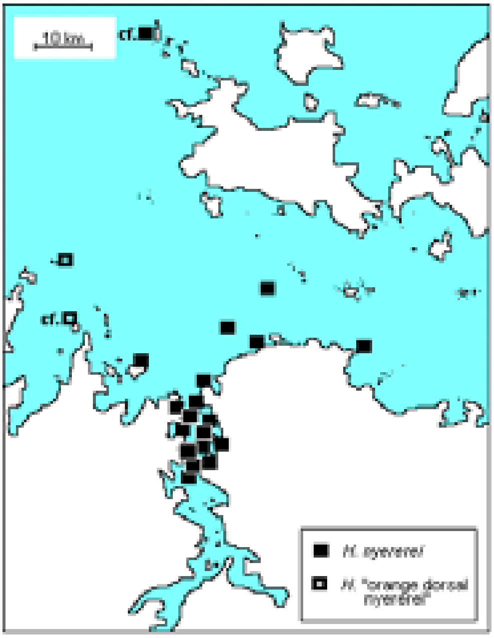

10 km
■ H."short scraper"
☐ H."large eye black"
▣ H."red anal blue"

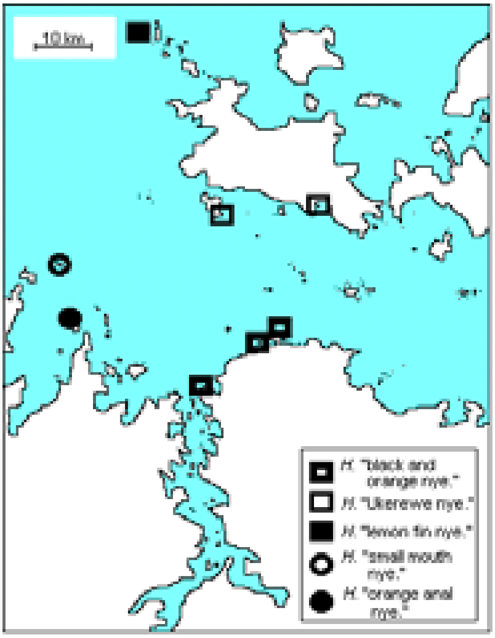

10 km
■ H. "carp"
● H. "orange carp"
☐ H. "red carp"
▣ H. cf. "red carp"

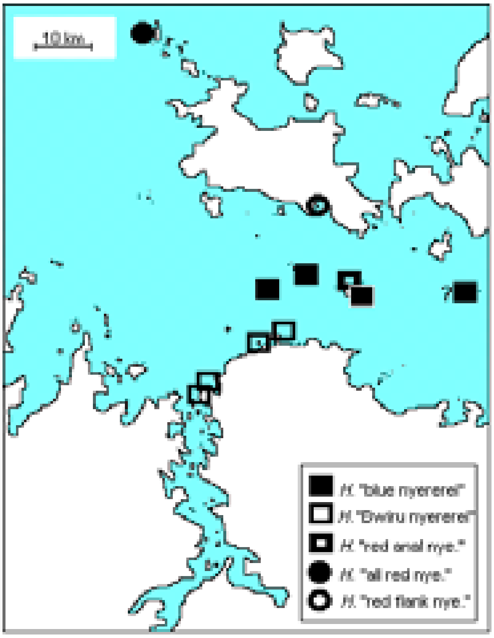

10 km
ZM
ZS
RC
?
■ H. "zebra nyererei"
▣ H. cf. zny x nye
● H. cf. zny-bbl
ZM H. "zebra Mlandere"
ZS H. "zebra Senga"
RC H. "red chest"

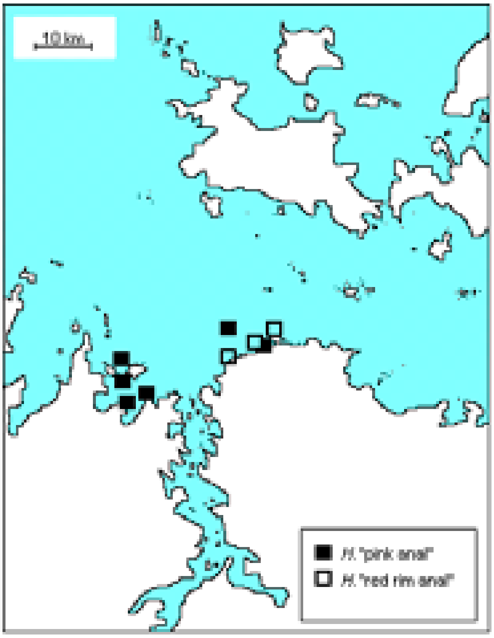

10 km
■ H. "big blue" red
▣ H. "big blue" blue
● H. "red head nye."

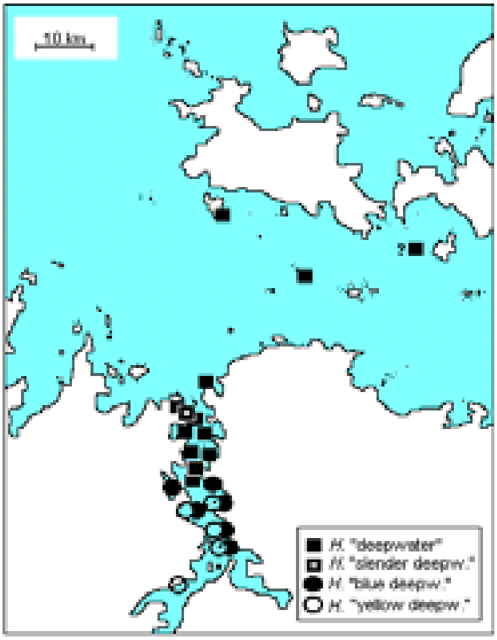

10 km
● H. "all black nye."

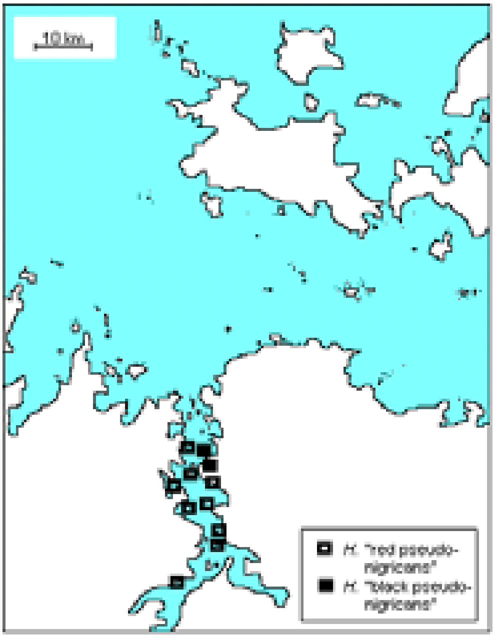

10 km
cf.
cf.
■ H. nyererei
▣ H. "orange dorsal nyererei"

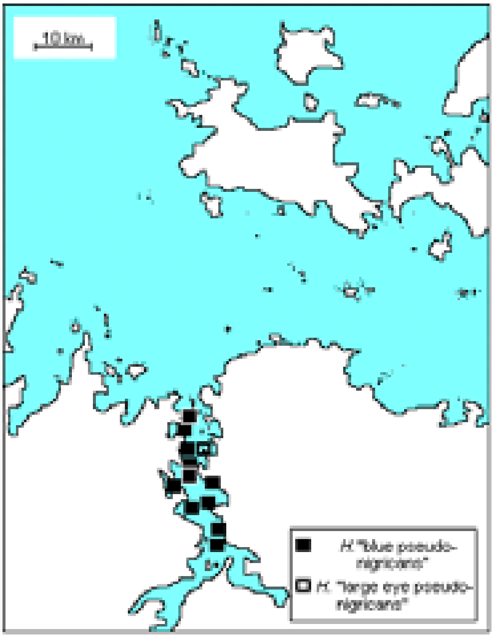

10 km
H. "black and orange nye."
H. "Ukerewe nye."
H. "lemon fin nye."
H. "small mouth nye."
H. "orange anal nye."

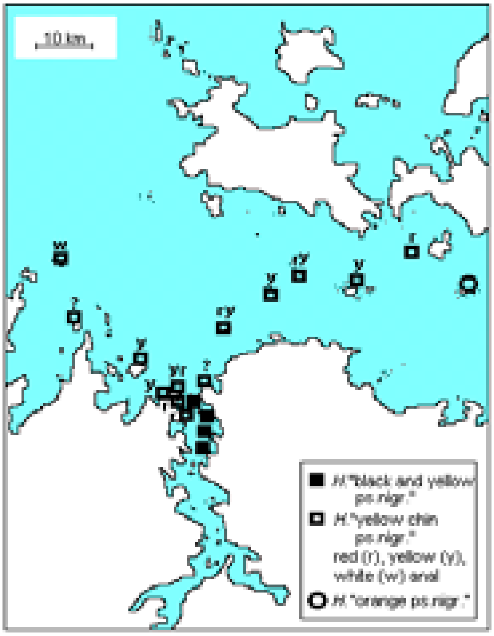

10 km
?
H. "blue nyererei"
H. "Dwiru nyererei"
H. "red anal nye."
H. "all red nye."
H. "red flank nye."

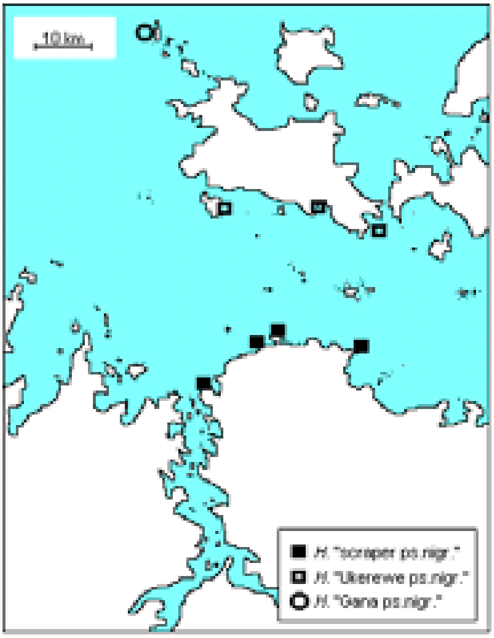

10 km
H. "pink anal"
H. "red rim anal"

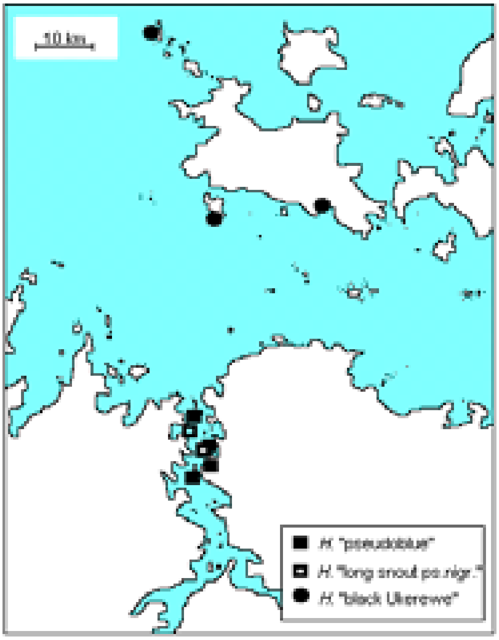

10 km
?
H. "deepwater"
H. "slender deepw."
H. "blue deepw."
H. "yellow deepw."

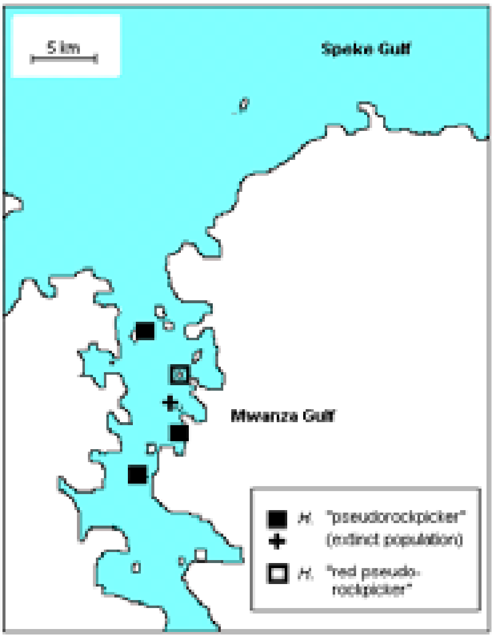

10 km
H. "red pseudo-nigricans"
H. "black pseudo-nigricans"

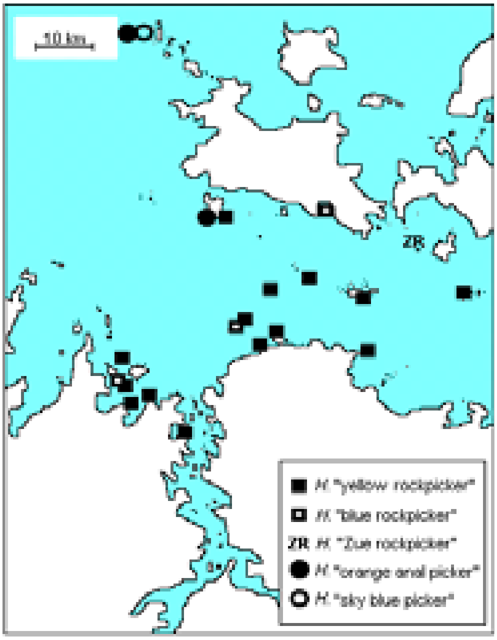

10 km
H."blue pseudo-nigricans"
H. "large eye pseudo-nigricans"

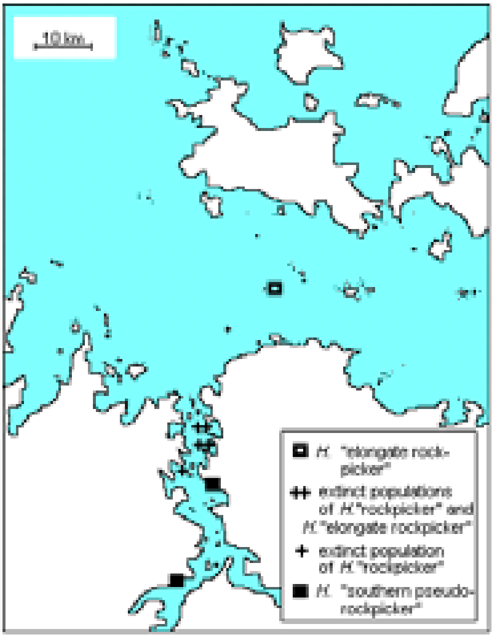

10 km
w
r
y
yr
r
r y
y
r y
y
r
H."black and yellow ps.nigr."
H."yellow chin ps.nigr."
red (r), yellow (y), white (w) anal
H."orange ps.nigr."

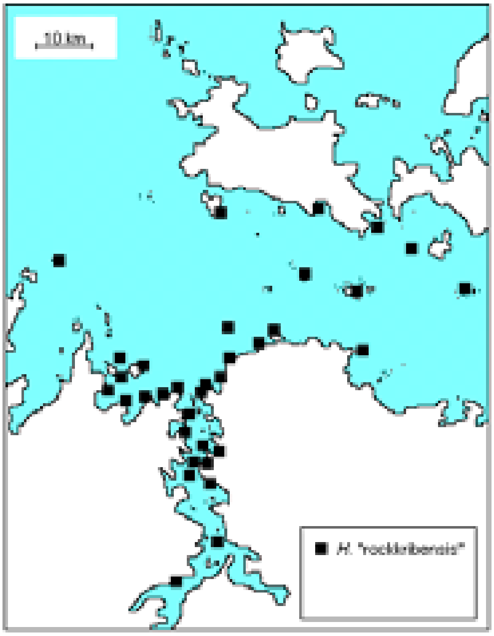

10 km
H. "scraper ps.nigr."
H. "Ukerewe ps.nigr."
H. "Gana ps.nigr."

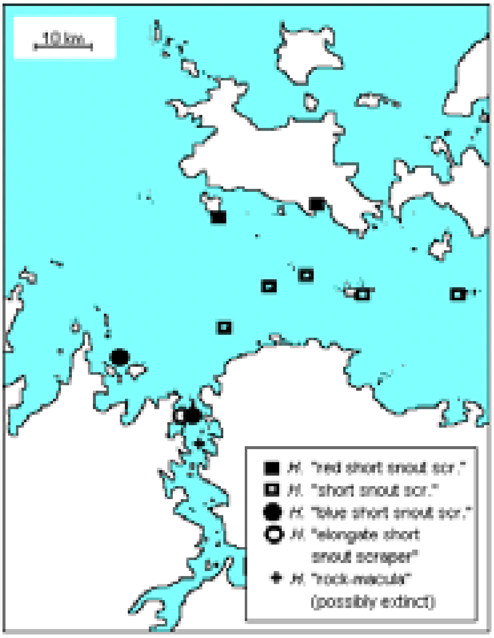

10 km
■ H. "pseudoblue"
▣ H. "long snout ps.nigr."
● H. "black Ukerewe"

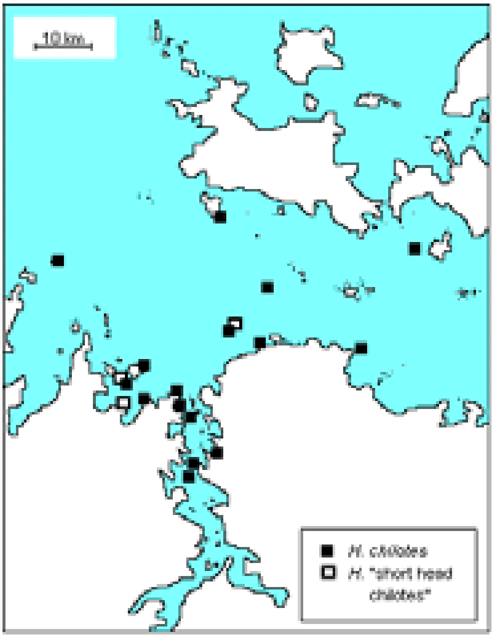

5 km
Speke Gulf
Mwanza Gulf
■ H. "pseudorockpicker"
✚ (extinct population)
□ H. "red pseudo-rockpicker"

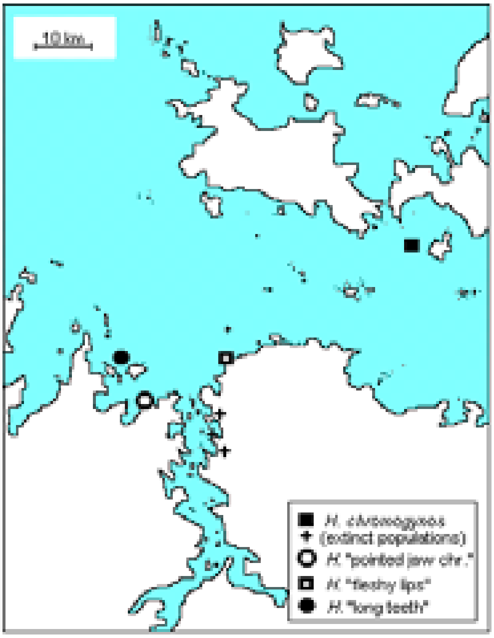

10 km
ZR
■ H. "yellow rockpicker"
▣ H. "blue rockpicker"
ZR H. "Zue rockpicker"
● H. "orange anal picker"
○ H. "sky blue picker"

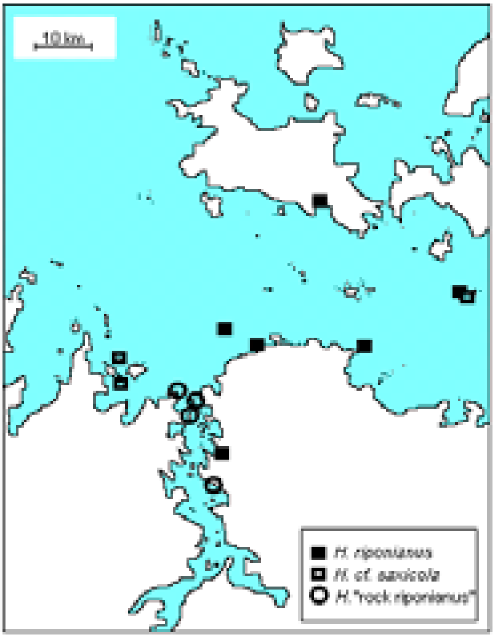

10 km
▣ H. "elongate rock-picker"
✚✚ extinct populations of H. "rockpicker" and H. "elongate rockpicker"
✚ extinct population of H. "rockpicker"
■ H. "southern pseudo-rockpicker"

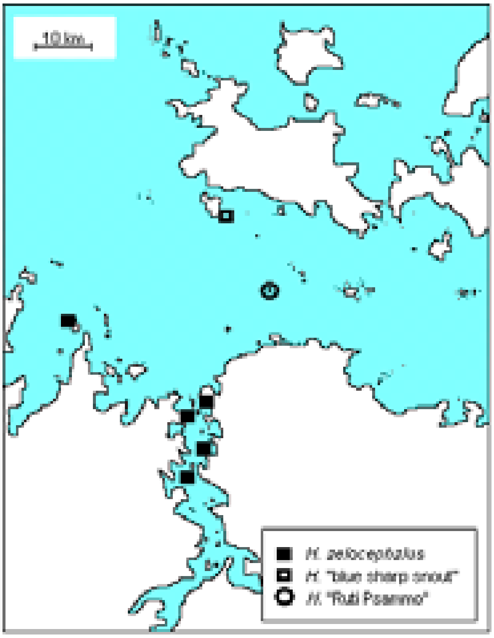

10 km
■ H. "rockkribensis"

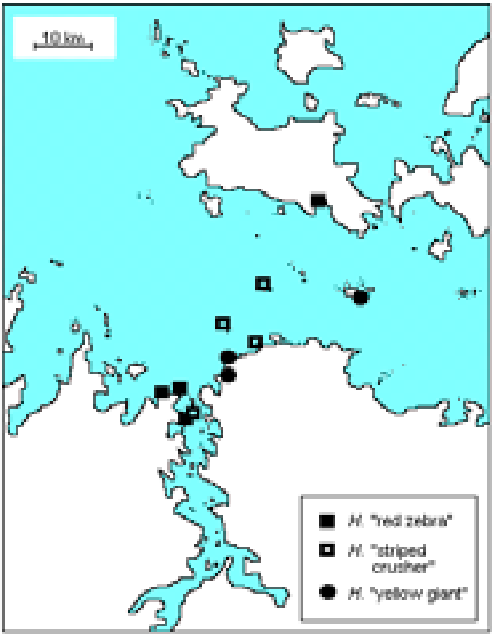

10 km
■ H. "red short snout scr."
▣ H. "short snout scr."
● H. "blue short snout scr."
○ H. "elongate short snout scraper"
✚ H. "rock-macula"
(possibly extinct)

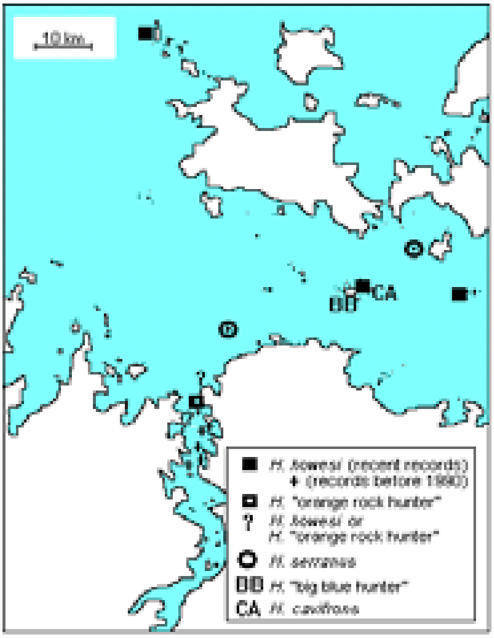

10 km
■ H. chilotes
☐ H. "short head chilotes"

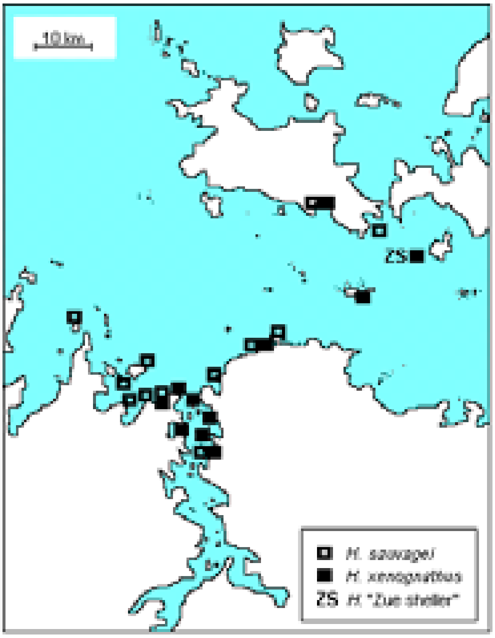

10 km
■ H. chromogynos
✚ (extinct populations)
○ H. "pointed jaw chr."
▣ H. "fleshy lips"
● H. "long teeth"

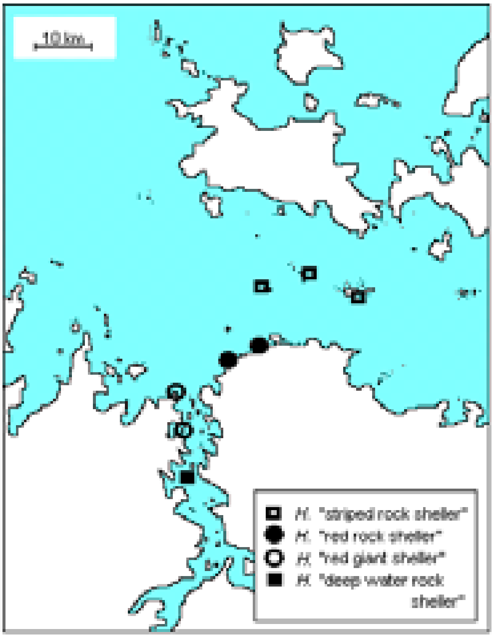

10 km
■ H. riponianus
▣ H. cf. saxicola
○ H. "rock riponianus"

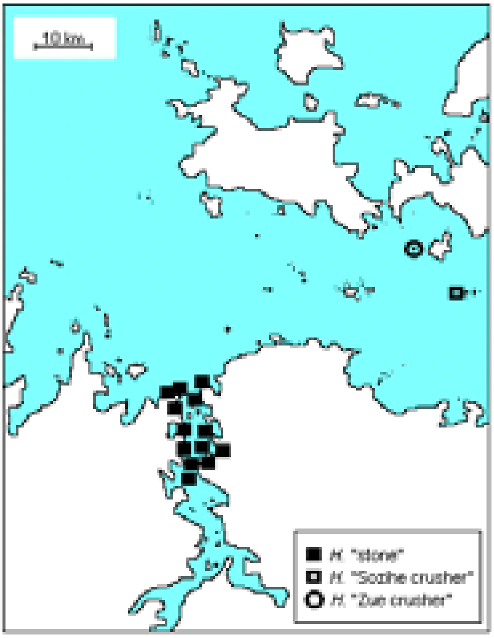

10 km
■ H. pelocephalus
▣ H. "blue sharp snout"
○ H. "Ruti Psammo"

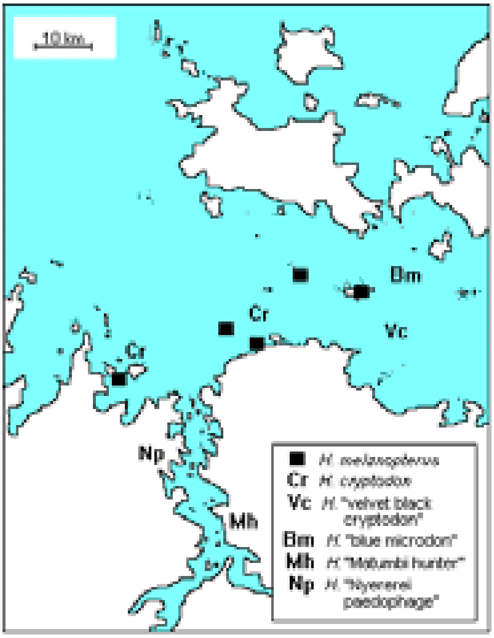

10 km
■ H. "red zebra"
▣ H. "striped crusher"
● H. "yellow giant"

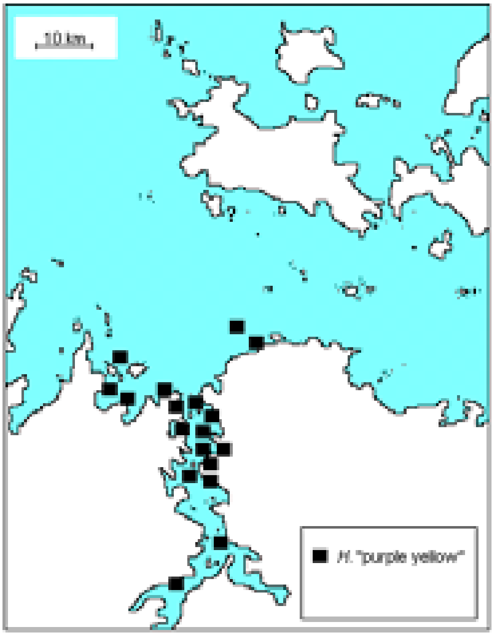

10 km
BB
CA
■ H. bowesi (recent records)
+ (records before 1980)
▣ H. "orange rock hunter"
? H. bowesi or
H. "orange rock hunter"
○ H. serranus
BB H. "big blue hunter"
CA H. cavifrons

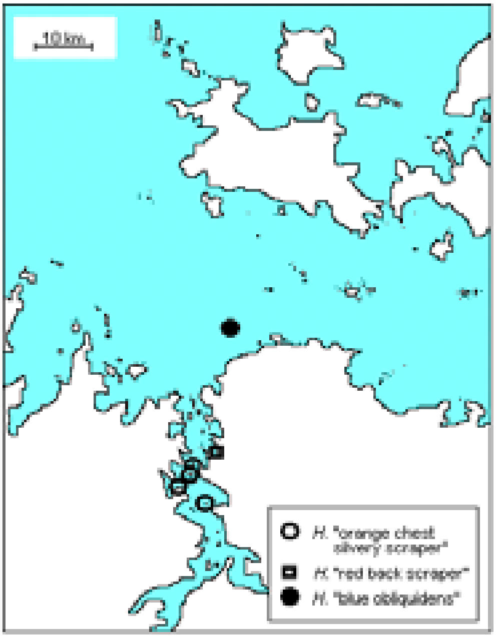

10 km
ZS
■ H. sauvagei
■ H. xenognathus
ZS H. "Zue sheller"

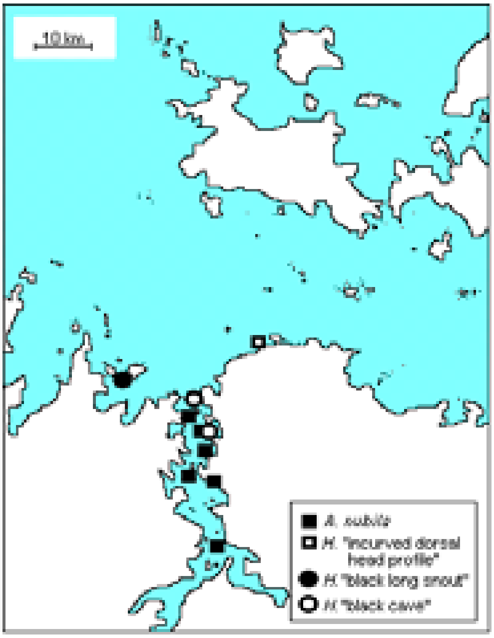

10 km
■ H. "striped rock sheller"
● H. "red rock sheller"
○ H. "red giant sheller"
■ H. "deep water rock sheller"


10 km
■ H. "stone"
■ H. "Scothe crusher"
○ H. "Zue crusher"


10 km
Bm
Cr
Vc
Cr
Np
Mh
■ H. melanopterus
Cr H. cryptodon
Vc H. "velvet black cryptodon"
Bm H. "blue microdon"
Mh H. "Mabumbi hunter"
Np H. "Nyererei paedophage"


10 km
■ *H.* "purple yellow"


10 km
○ *H.* "orange chest silvery scraper"
◘ *H.* "red back scraper"
● *H.* "blue obliquidens"


10 km
■ *A. nubila*
◘ *H.* "incurved dorsal head profile"
● *H.* "black long snout"
○ *H.* "black cave"

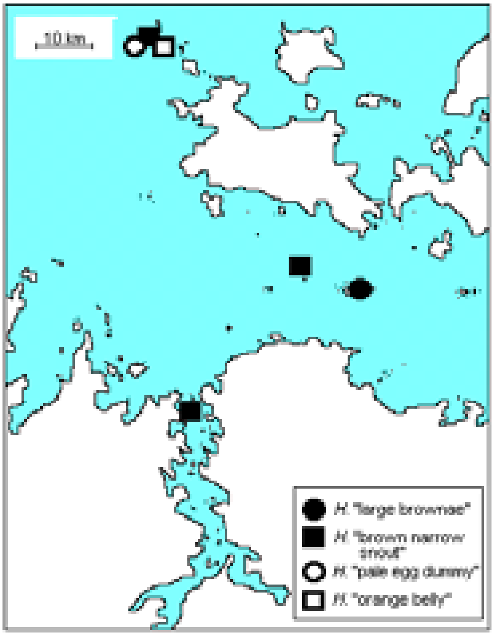

10 km
● *H.* "large brownae"
■ *H.* "brown narrow snout"
○ *H.* "pale egg dummy"
□ *H.* "orange belly"

Table 3

Taxonomic measurements of rock-dwelling haplochromines

Explanations

The table contains a set of morphometric measurements and qualitative characteristics of the dentition that were found to be useful for species identification. For described and undescribed species the values obtained in this study are shown. They can deviate from values given by other authors (see table 4).The table is at places incomplete because not all measurements could be taken yet.

For the definition of measurements see the chapter on identification, and Barel *et al.* 1977.

SL = standard length, BD = body depth, HL = head length, JR = lower jaw length/width ratio, LJL = lower jaw length, EL = eye length, IOW = inter orbital width. Values are mean values, except for SL. SL is the maximum of the random sample of adult males used for these measurements. Thus, it is not necessarily the maximum attained SL of a species but merely an orientation help.

OT, IR, and gap are dentition characters. Values in front of an oblique bar refer to the lower jaw, those behind it refer to the upper jaw. Only one value indicates equal conditions in both jaws.

OT = shape of anterior teeth in the outer tooth row: 1 = equally bicuspid, 2 = subequally bicuspid, 3 = unequally bicuspid, 4 = eakly bicuspid, 5 = unicuspid, ° indicates obliquely truncated cusp shape (see page 59).

IR = number of inner rows. A mean value between two integers indicates a range between the two integers, if ranges are larger, they are given instead of the mean.

gap = the width of the gap that separates the outer tooth row from the first inner row: - = no gap, + = small, ++ = moderate, +++ = wide gap.

	SL	BD	HL	JR	LJL	EL	IOW	OT	IR	gap
Vertical bar *Mbipi*										
***Neochromis* complex**										
H. (Neochromis) nigricans	92.6	37.4	32.3	1.0	34.5			2/2	5-6/5-7	-/-,+
H. (Neochromis) "short head nigricans"	114.7	34.6	29.3	1.0	33.2	27.1		1.8/1.8	4-6/5-6	-,+/+
H. (Neochromis) "large eye nigricans"										
H. (Neochromis) "giant scraper"	143.9		30.7	1.2	36			2/2	3-8/5-8	-,+/+
H. (Neochromis) "red tail giant scraper"	120.9	37	29.3	1.04	33.9	24.0				
H. (Neochromis) "black tail giant scraper"	118.2	39.3	30.4	1.07	34.0	23.9				
H. (Neochromis) "blue scraper"	105.2	35.7	31.1	1.0	35.9			2-3/2	4-6/5-7	-/-,+
H. (Neochromis) "eastern blue scraper"										
H. (Neochromis) "Juma scraper"	99.6	36.8	31.4	1.05	37.7	24.9		2/2	4-6/5-6	-/-,+
H. (Neochromis) "Vesi scraper"	105.7	38.5	31.0	1.0	36.8			2/2	4-8/6-9	-,+/+
H. (Neochromis) "yellow anal scraper"	102.0	36.0	30.6	1.05	36.0			2/2	4-5/5-6	+/+
H. (Neochromis) "long black"	101.0	30.4	29.8	1.1	36.7			2/2	4-5/4-5	-,+/+
H. (Neochromis) "Labeo scraper"										
H. (Neochromis) "black nigricans"	109.7	38.6	30.1	0.93	36.8			2/2	4-6	-,+
H. (Neochromis) "velvet black"	115.2	36.04	31.2	1.13	35.9			1-4/1-4	4-6/4-6	-,+/+,++
H. (Neochromis) "unicuspid scraper"	91.02	30.7	30.8	1.30	38.1			2-5/2-5	3-4/3-5	+,++,+++
H. (Neochromis) "Bihiru scraper" bicuspid morph	135.3		30.3	1.20	35.8			2-5/2-5	2-5/3-5	+,++,+++
H. (Neochromis) "Bihiru scraper" unicuspid morph	122.5		32.1	1.31	40.8			(4-)5/(4-)5	2-4/2-5	++,+++
H. (Neochromis?) "pseudoblack"	83.6	33.8	31.6	1.45	36.7			2-3/2-3	2-5/2-6	++/++
***Xystichromis* like algae scrapers**										
H. (Xystichromis) "copper black"	38.4	33		1.30	38.5	24.7	28.4	2-3/2-3	3-5/4	+/++
H. (Xystichromis) "short scraper"	78.9	36.3	35.3	1.32	38.4	24.0	24.1			
H. (Xystichromis) "red anal blue"	96.33	36.9	31.9	1.3	36.8	23.3	27.0			
H. (Xystichromis) "large eye black"	98.6	37.9	34.5	1.49	40.9	30.5	28.3	2-3	3/2-3	
H. (Xystichromis) "carp"	118.0	38.1	32.6	1.2	40.7	22.8	29.1	3.9/3.9	3-7/3-6	++/++,+++
H. (Xystichromis) "orange carp"										
H. (Xystichromis) "red carp"	115.0	37.5	32.3	1.44	39.2	23.6	26.8		2-5/4-6	+,++,+++

	SL	BD	HL	JR	LJL	EL	IOW	OT	IR	gap
***Nyererei* complex**										
H. (?) nyererei	103.7	38.4	33.2	1.53	42.6	25.2	26.1	4.9/4.9	2-3/2-4	++,+++
H. (?) "black and orange nyererei"	91.8	32.3	32.4	1.68	41.2	24.7	27.3	4.7/4.5		
H. (?) "orange anal nyererei"	125.2	37.7	32.0	1.25	41.8	23.7	26.4	5/5	2-3	
H. (?) "small mouth nyererei"	109.8	40.6	31.3	1.64	40.7	24.8	27.2	5/5		
H. (?) "Ukerewe nyererei"	96.7	38.7	33.4	1.50	41.4	25.3	26.3	5/5		
H. (?) "lemon fin nyererei"	133.0	38.7	31.7	1.35	41.6	21.8	30.0	5/5		
H. (?) "orange dorsal nyererei"	89.1	36.0	31.4	1.78	39.4	24.0	29.1	5/5		
H. (?) "zebra nyererei"	110.3	38.7	35.1	1.55	43.4	23.1	25.2	5/5	2-3/2-4	++
H. (?) "big blue"	113.1	39.5	33.7	1.43	43.5	21.8	23.8	4/3	2-3/3-4	+++
H. (?) "big blue" red	109.8	37.6	32.1	1.42	42.6	23.1	26.3	4.2/4.1	2-3/3-4	++,+++
H. (?) "red head nyererei"	96.5	34.5	33.2	1.44	43.2	23.1	23.6			
H. (?) "zebra Miandere"	110.6	37.6	31.6	1.44	41.1	23.8	28.3	5/5		+++
H. (?) "zebra Senga"	96.5	35.5	34.2	1.37	38.8			3.8/3.8	2-3	+++
H. (?) "all black nyererei"	77.0		36.2	1.33	39.7			5/5	2-3/2-5	+++
H. (?) "blue nyererei"	89.5	35.9	32.5	1.50	38.5	25.8	25.1	4.9/4.9	2-3/2-3	
H. (?) "pink anal"	87.5	36.8	32.7	1.5	38.6	22.9	24.0	5/4.7	2.2/2.3	+++
H. (?) "red rim anal"	97.2	37.0	32.5	1.6	37.9	25.7	26.4	4.5/4.5	2/3	
H. (?) "red anal nyererei"	97.0	34.8	31.6	1.49	38.0	26.1	24.5	5/4.2	2-3/2-5	
H. (?) "Bwiru nyererei"	105.7	33.8	33.0	1.39	40.2	25.0	25.0			+++
H. (?) "red flank nyererei"	87.9	37.7	32.2	1.62	39.2	24.1	24.5			
H. (?) "all red nyererei"	100.0	37.5	31.6	1.37	40.4	25.3	24.8			
***Haplochromis* "pseudonigricans" complex**										
H. (?) "yellow chin pseudonigricans"	103.9	35.5	31.9	1.41	38.0	26.9	22.3	3.9/3.6	2-3	+++
H. (?) "orange pseudonigricans"	96.0	38.3	32.3	1.5	36.8	27.4	23.8	4.8/4		
H. (?) "black and yellow pseudonigricans"	85.1	36.5	31.7	1.42	35.2	27.9	22.1	4.6	2.56	
H. (?) "large eye pseudonigricans"	91.1	36.8	31.8	1.2	37.5	30.2	23.8	3.6/3.9		
H. (?) "blue pseudonigricans"	95.6	37.6	33.1	1.6	37.8	27.3	23.3	2.8/2.7	2/2-3	
H. (?) "red pseudonigricans"	80.1	37.9	33.1	1.7	38.1	25.8	22.4	2.8/2.6	2-3/2-3	+++
H. (?) "scraper pseudonigricans"	101.4	35.4	32.2	1.4	36.9	28.3	24.4	2.4/2.2	3-4/3-5	+/++,+++
H. (?) "Ukerewe pseudonigricans"	98.8	36.6	31.3	1.5	37.4	25.1	26.4	2.8/2.8		
H. (?) "Gana pseudonigricans"	95.8	34.7	30.0	1.4	37.4	25.7	24.9	3.5/3.5		
H. (?) "black Ukerewe"	103.0	35.5	32.5	1.59	38.9	26.4	21.9	4.2/3.7	3/3	++,+++/+++
H. (?) "long snout pseudonigricans"	92.6	37.4	33.4	1.6	41.2	25.5	21.0	4/3.6	2-3	+++
H. (?) "pseudoblue"	92.4	37.7	33.7	1.7	41.1			4.2/4.2	2/3	+++
***Haplochromis* "deepwater" complex**										
H. (?) "deep water"	116.2	39.6	34.2	1.8	42.3	23.0	23.6	4.6/4.6	2/3	++,+++
H. (?) "blue deep water"	101.0	38.8	34.0	1.52	39.7	22.4	23.8	4/4	3.6/4.3	+++
H. (?) "yellow deepwater"	99.0	36.3	34.2	1.4	41.0			4.3/4	3/3.6	+++
H. (?) "slender deep water"	105.4	36.5	32.7	1.9	42.4	26.5	22.6	4.8/4.8	2.5/3	
Chessboard *Mbipi*										
Paralabidochromis "rockpicker" complex										
H. (Paralabidochromis) "pseudorockpicker"	88.7	37.4	31.7	1.28	32.8	30.3	23.0	4.8/4.6	2-3	++,+++
H. (Paralabidochromis) "red pseudorockpicker"	83.7	34.5	29.9	1.27	33.2	24.4	19.6		3.5	
H. (Paralabidochromis) "southern pseudorockp."	85.0	36.7	32.1	1.31	34.3			2.8/2.8	2	++,+++
H. (Paralabidochromis) "chessboard picker"	77.0	34.8	31.2	1.39	31.2	26.2	20.1	5/5	2/2.5	
H. (Paralabidochromis) "yellow pseudorockpicker"	99.1	36.8	30.1	1.07	29.0	25.5	25.4	3.3/2.6	2.5/2.8	(++),+++
H. (Paralabidochromis) "Zue rockpicker"	89.1	36.2	30.6	1.14	28.8	29.8	26.6	4.5/3.5	3.5/3	
H. (Paralabidochromis) "rockpicker"								2-5	3-4(5)	+
H. (Paralabidochromis) "elongate rockpicker"	91.03	32.5	29.6	1.11	31.9	25.3	22.4	2/2	5/5	
H. (Paralabidochromis) "orange anal picker"	110.2	33.5	28.0	1.11	28.5	26.0	24.9	3.3/2.9	3.6/4.1	
H. (Paralabidochromis) "blue rockpicker"	114.5	36.6	30.1	1.16	30.7	26.4	24.6	2.8/2.2	3.7/4.3	+,++
H. (Paralabidochromis) "sky blue picker"	97.7	34.5	29.3	1.3	35.0	26.5	26.1	2	4/4	+/++
***Paralabidochromis* "rockkribensis" complex**										
H. (Paralabidochromis) "rockkribensis"	102.0	37.3	32.3	1.32	38.9	23.7		2.5/2.2	3-4/3-5	+,++/++,+++
H. (Paralabidochromis) "short snout scraper"	111.2	37.8	31.9	1.16	34.5	27.2	24.6	2.8/2.6	2.2/2.7	++,+++
H. (Paralabidochromis) "red short snout scraper"	105.7	41.1	32.0	1.3	36.1	26.2	27.7	3.8/3.3	2.8/3.5	+,++,+++
H. (Paralabidochromis) "elongate short snout scr."	90.4	33.4	31.6	1.6	35.6	26.0	23.8	2.8/2.8	2.5/3	+/+,++
H. (Paralabidochromis) "rock macula"	95.3	37.0	30.8	1.3	34.0	26.9	23.7	2.4/2.4	2.3/2.1	
H. (Paralabidochromis) "blue short snout scraper"	125.6	38.1	31.6	1.2	35.1	25.0	27.4	2.6/2.6	3.5/3.8	+,++

	SL	BD	HL	JR	LJL	EL	IOW	OT	IR	gap
***Paralabidochromis chilotes* complex**										
H. (Paralabidochromis) chilotes	121.5	37.6	36.8	1.43	41.0	21.2	21.8	5/5	2-3/3-4	
H. (Paralabidochromis) "short head chilotes"	127.6	36.8	33.0	1.31	34.7	22.5	21.3	5/4.7	2/3-4	+++
***Paralabidochromis chromogynos* complex**										
H. (Paralabidochromis) cf. chromogynos	95.8	35.5	34.1	1.27	36.0	26.0	25.4	5/5	5/5	+++
H. (Paralabidochromis) "pointed jaw chromogynos"	90.5	39.2	36.4	1.26	35.3	24.2	22.7	3/3	2/2	++
H. (Paralabidochromis) "fleshy lips"	87.3	35.6	35.0	1.4	37.4	26.9	20.6	5/5	3/4	++
H. (Paralabidochromis) "long teeth"	85.0	33.7	35.1	1.53	38.0	27.6	21.2	5/5	3/3.5	+++/++
Psammochromis										
H. (Psammochromis) riponianus	117.6	35.6	34.0	1.3	37.3			5/5	3.5/3.75	
H. (Psammochromis) "rock riponianus"	100.0	37.1	33.1	1.5	37.7	23.9	23.8	4.5/4.5	2/2.8	++,+++
H. (Psammochromis) cf. *saxicola*	118.8	36.9	34.1	1.7	39.0	25.9	21.1	4.3/4.3	2.3/2.6	+++
H. (Psammochromis) aelocephalus	124.6	37.2	35.9	1.7	43.9	25.0	22.8	4.3/4.3	2.2/2.2	++,+++
H. (Psammochromis) "red zebra"	100.7	36.9	32.2	1.49	38.8	26.9	22.9	4.3/4	3/3.5	++/+++
H. (Psammochromis) "Ruti-Psammo"	89.1	36.5	33.8	1.8	41.4	28.6	21.6	4/4	2.5/3	++
H. (Psammochromis) "striped crusher"	92.7	34.9	34.3	1.55	37.8	24.5	21.5	4.2/3.7	2/2	++/+++
H. (Psammochromis) "blue sharp snout"	115.1	43.3	34.3	1.47	40.1	23.3	27.1	5/5	2/3	+++
H. (?) "yellow giant crusher"	132.1	36.7	32.7	1.4	38.6	23.0	23.1	5/5	3.2/3.7	++/+++
***Astatotilapia*-like insect eaters**										
Astatotilapia nubila	79.1	39.8	35.7	1.74	41.7	28.5	26.5	3.1/3.3	2.3/3	++,+++
H. ("Astatotilapia") "incurved dorsal head profile"	100.1	37.2	34.5	1.51	39.0	25.4	25.9	3.8/3.3	3.3/3	++/+++
H. ("Astatotilapia") "black long snout"	61.3	36.0	35.7	1.95	38.4	27.6	21.2	3/3	2/3	+++
H. ("Astatotilapia") "black cave"	72.8	34.7	33.2	1.82	38.8	31.2	22.9	3.3/3	2/2	++
H. ("Astatotilapia") "large brownae"	119.3	32.8	31.0	1.39	36.3	24.5	24.0	4.3/4.1	2.3/2.7	++/+++
Ungrouped insect eaters										
H. (?) "brown narrow snout"	100.2	35.6	33.1	1.7	39.0	26.8	22.0	4/4	2/3	
H. (?) "pale egg dummy"	89.8	36.5	32.2	1.39	39.6	25.1	21.7			
H. (?) "orange belly"	90.5	37.5	32.2	1.51	41.2	27.2	24.7	4.8/4.5	3/3.5	++,+++
Double stripe complex										
H. (?) thereuterion	69.8	26.0	34.1	2.69	39.6	29.0	19.8	3/3	2/2	+++
Snail crushers										
H. (Labrochromis) "stone", red & blue	144.9	38.3	33.7	1.39	39.9	24.6	26.7	5/5	2/2.25	++,+++/+++
H. (?) "Zue crusher"	118.4	37.4	33.3	1.42	37.0	25.7	24.1	5/5	2/2	++/+++
H. (?) "Ukerewe crusher"	103.1	39.4	32.8	1.28	36.3	24.9	25.5	4.5/4.5	2/2.5	+++
Snail shellers										
H. (Ptyochromis) xenognathus "rocks"	111.8	36.7	31.5	1.4	34.8			5/5	4.5/5.5	+++
H. (Ptyochromis) "striped rock sheller"	124.4	34.4	33.7	1.12	35.8	26.9	27.8	5/5	4.75/5.5	++/++,+++
H. (Ptyochromis) "deep water rock sheller"	111.3	39.7	33.0	1.1	35.0	27.2	23.6	5/5	3-4/4-5	+++
H. (Ptyochromis) "red giant sheller"	118.6	38.5	32.2	1.24	38.5	25.2	25.0	5/5	3.5/4.5	+,++/++,+++
H. (Ptyochromis) "Zue sheller"	101.4	32.4	32.4	1.56	37.0	26.4	24.8	4.7/4.5	2.3/3	++,+++/+++
H. (Ptyochromis?) "red rock sheller"	82.6	34.3	31.1	1.4	37.0	28.6	22.4	3/3.5	2/2	+/+++
Fish eaters										
H. (Harpagochromis) cavifrons	116.6	32.5	35.5	1.78	45.2	23.2	19.5	5/5	2/3	+++
H. (Harpagochromis) serranus "rocks"	156.0	32.0	36.8	2.06	48.1	19.7	18.9	5/5	1.8/2.8	+++
H. (Harpagochromis) "big blue hunter"	145.7	32.4	35.3	1.78	46.9	23.6	22.1	5/5	2.3/3.5	+++
H. (Harpagochromis) howesi	129.1	32.8	35.3	2.04	46.5	24.6	19.6	5/4.9	2/2	++,+++/++,+++
H. (Harpagochromis) "orange rock hunter"	109.0	33.2	36.8	1.91	43.5	27.0	17.3	5/5	2/2	++,+++/+++
Paedophages										
H. (Lipochromis) cryptodon	103.7	28.8	31.5	1.45	42.8	23.9	23.7	5/4.8	1/1	+++
H. (Lipochromis) "velvet black cryptodon"	125.6	28.4	32.1	1.38	42.1	23.7	24.8	5/5	2	+++
H. (Lipochromis) "blue microdon"	73.1	37.7	33.5	1.52	42.9	29.6	22.2	4.8/4.5	2/2	++/+++
H. (Lipochromis) cf. melanopterus	96.8	35.3	32.9	1.13	40.5	29.6	26.9	5/4.9	1.5/1.5	++/+++
H. (Lipochromis) "matumbi hunter"	85.1	28.3	31.0	1.3	41.4	25.6	26.5	5/5	2/2	++
H. (?) "nyererei paedophage"	94.3	38.9	31.7	1.29	40.8	28.3	28.1	5/5	2/2	++

	SL	BD	HL	JR	LJL	EL	IOW	OT	IR	gap
Algae scrapers of the *Haplochromis* lineage										
H. (Haplochromis) "blue obliquidens"	106.6	36.9	32.3	1.40	39.1	27.6	30.0	4°/3.9°	3.5/3.6	-,+,++/++,+++
H. (Haplochromis) "purple yellow"		36.4	33.4	1.50	36.5	28.2	29.7	2.8°/3°	3.2/4.3	+,++
H. (Haplochromis) "red back scraper"		36.0	36.5	1.48	40.0	30.7	27.1	3°/3°	2.8/3	++/++,+++
H. (Haplochromis) "orange chest silvery scraper"	80.0	38.8	35.0	1.39	41.8			3/3	3/3	++/+++

Table 4:

Taxonomic measurements of described rock-dwelling haplochromines

Morphometric and dentition data of described haplochromine species that occur frequently or exclusively at rocky shores. All data are taken from Greenwood´s descriptions and re-descriptions (all references in the text), except those for *H. (?) nyererei*, *H. (Harpagochromis) howesi,* and *H. (?) thereuterion*, which are taken from Witte-Maas & Witte 1985, van Oijen 1992, and van Oijen & Witte 1996 respectively. If mean values were not available, either modal values (if available), or ranges are given. In none of the original descriptions, except those of *H. (?) nyererei* and *H. (?) thereuterion*, were sexes measured separately. For *H. (?) nyererei* and *H. (?) thereuterion* the values of males are given, to enhance comparison with the data in table X. For *H. (H.) howesi* only the values for fishes above 110mm SL are given, to enhance comparison with the data in table 3. For abbreviations and further explanations see table 3.

	SL	BD	HL	JR	LJL	EL	IOW	OT	IR	gap
Vertical bar *Mbipi*										
H. (Neochromis) nigricans	94	36.9	31.2	1.2	35.6	30.0	28.8	2,3	3-7	-,+
H. (Xystichromis) nuchisquamulatus	113	37.9	31.8	1.5	37.6	29.6	29.3	3	3-6/4-8	+
H. (?) nyererei	86	39.9	33.4	1.45	37.5	29.2	5.2	3	2-4/3-5	++
Chessboard *Mbipi*										
H. (Paralabidochromis) victoriae	76	33.0	31.6	-	-	29.2	25	5/5	4/3	
H. (P.) chilotes "lobed lips"	148	32.5-40.8	35.5	-	39.6	25.4	23.8	4-5	2-3(1,4)	
H. (P.) chilotes "non-lobed lips"			32.7	-	33.2	-	-	-	-	-
H. (P.) chromogynos	110	35.0	33.2	1.3	32.5	28.6	27.5	4-5	3(2,4)	-
Psammochromis										
H. (Psammochromis) riponianus	104	35.7	35.7	1.6-8	38.5	26.6	25.1	3-5	(1)2-4/(2)3-4	
H. (Psammochromis) saxicola	123	37.8	37.8	1.8	43.0	24.4	26.9	(4-)5	2-3(4,5)	
H. (Psammochromis) aelocephalus	120	31.3-38.4	33.0-38.6	1.8-2.0	41.2-45.1	24.5-27.8	24.8	4-5	(2)3-5/3-6	
***Astatotilapia*-like species**										
Astatotilapia nubila	86	36.8	34.2		39.2	28.4	25.2	3	2-3/2-5	++
H. ("Astatotilapia") brownae	104	35.1	31.6	2.0	40.3	28.6	29.8	3(4,5)	1-2/2-3(4)	
H. ("Astatotilapia") barbarae	106	34.0	33.5	1.5-7	38.0	25.5	25.8	3	2(3)/2-3	
Double stripe complex										
H. (?) thereuterion	82	26.5	33.5	2.6	41.2	27.8	19.5	3,4,5	2/2	+++
Snail eaters										
H. (Ptyochromis) sauvagei	105	35.6	31.9	1.3	34.5	28.9	27.0	(4,)5	2-6/3-8	++
H. (Ptyochromis) xenognathus	113	34.8	33.1	1.4	34.5	26.0	26.8	5	3-9	
Astatoreochromis alluaudi	163	33.8-43.3	35.0	1.5-6	40.0	22.1	28.3	4-5	1-2	

	SL	BD	HL	JR	LJL	EL	IOW	OT	IR	gap
Fish eaters										
H. (Harpagochromis) cavifrons	195	35.6	37.3	2.0	55.5	20.3	25.4	5	1-2(3)/(1)2-4	
H. (Harpagochromis) serranus "rocks"	205	36.0	36.3	2.0	54.3	23.3	23.3	5(4)	2(1,3)/2-3(4)	
H. (Harpagochromis) howesi	163.3	34.8	36.4	2.4	49.7	22.5	21.2	5	2(3)/2(1,3)	
Paedophages										
H. (Lipochromis) cryptodon	130	27.5-35.6	30.3-34.9	1.5-6	42.3	25.8	23.6	5(3,4)	1-2	
H. (Lipochromis) melanopterus	127	35.5	33.5	1.3	37.6	28.2	27.0	5	2	
H. (Lipochromis) maxillaris	160	32.0-42.8	30.0-34.8	1.5-8	50.0	27.3-33.2	26.5	5	1(2)	+
H. (Lipochromis) obesus	170	33.6-47.3	30.3-35.9	1.3	40.0-54.5	27.6	32.2	3,4,5	1(2)	+
Algae scrapers of the *Haplochromis* lineage										
H. (Haplochromis) obliquidens	89	37.5	32.3	1.4	37.2	31.4	31.8	4°,5°	2-4	++
H. (Haplochromis) lividus	90	36.5	32.7	1.6	37.2	31.4	29.7	3°	2-4/2-5	++/+-

References

Akiyama, T., A.A. Kajumulo and S. Olsen. 1977. Seasonal variations of plankton and physicochemical condition in Mwanza Gulf, Lake Victoria. *Bull. Fresh. Fish. Res. Lab.* 27: 49-60.

Baerends, G.P. and J.M. Baerends-van Roon. 1950. An introduction to the study of ethology of cichlid fishes. *Behaviour (Supp.)* 1: 1-243.

Bailey, M. 1993. The undergravel filter. In: Konings, A. (ed). *Enjoying Cichlids.* Cichlid Press, St. Leon Rot: 31-33

Balirwa, J.S. 1984. *Ecological Separation in Barbus species in Lake Victoria*. M.Sc. thesis, University of Dar es Salaam, 155 pages.

Barel, C.D.N., M.J.P. van Oijen, F. Witte and E.L.M. Witte-Maas. 1977. An introduction to the taxonomy and morphology of the haplochromine cichlidae from Lake Victoria. *Neth. J. Zool.* 27: 333-389.

Barel, C.D.N. 1983. Towards a constructional morphology of cichlid fishes (teleostei, perciformes). *Neth. J. Zool.* 33: 357-424.

Barel, C.D.N., W. Ligtvoet, T. Goldschmidt, F. Witte and P.C. Goudswaard. 1991. The haplochromine cichlids in Lake Victoria: an assessment of biological and fisheries iinterests. In: Keeleyside, M.H.A. (ed). *Cichlid Fishes, Behaviour, Ecology, and Evolution*. Chapman and Hall: 258-279.

Bentzen, P. and J.D. McPhail. 1984. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): specialization for alternative trophic niches in the Enos Lake species pair. *Can. J. Zool.* 62: 2280-2286.

Bentzen, P., M.S. Ridgway and J.D. McPhail. 1984. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): spatial segregation and seasonal habitat shifts in the Enos Lake species pair. *Can. J. Zool.* 62: 2436-2439.

Bleher, H. in press. *The Fresh- and Brackish Water Fishes of the World*.

Boehme, A. 1996. Erfahrungen bei der Pflege von Viktoriasee-Buntbarschen. *DCG-Info (German Cichlid Association)* 27: 8-12.

Boulenger, G.A. 1906. Descriptions of new fishes discovered by Mr. E. Degen in Lake Victoria. *Ann. Mag. nat. Hist.* 17: 433-452.

Boulenger, G.A. 1911. On a third collection of fishes made by Dr. E. Bayon in Uganda, 1909-1910. *Ann. Mus. Genova* 45: 64-78.

Bouton, N., O. Seehausen, J.J.M. van Alphen and F. Witte. submitted. Trophic niche segregation among rock-dwelling haplochromines (Pisces: Cichlidae) from Lake Victoria. submitted to *Oecologia*.

Bwathondi, P.O.J. and G.C. Mahika. 1996. Distribution and infestation density of the weed *Eichhornia crassipes* on the Tanzanian shores of Lake Victoria. *Bull. Tanz. Fish. Res. Inst.* in press.

Cadwalladr, D.A. 1965. Notes on the breeding biology and ecology of *Labeo victorianus* Boulenger (Pisces: Cyprinidae) of Lake Victoria. *Rev. Zool. Bot. afr.* 72: 109-134.

Cooke, H.B.S. 1958. Observations relating to quarternary environments in East and South Africa. *Trans. Proc. geol. Soc. S. Afr.* 60, Annexure No. 5: 1-73

DeMason, L. 1996a. What´s new across the world. *Cichlid News* 5 (1): 28.

DeMason, L. 1996b. Cover photo. *Cichlid News* 5 (2): 1.

Dominey, W.J. 1984. Effects of sexual selection and life history on speciation: species flocks in African cichlids and Hawaiian *Drosophila*. In: Echelle, A.A. and I. Kornfield (eds). *Evolution of Fish Species Flocks*. University of Maine at Orono Press, Orono, Maine: 231-249.

Dorit, R.L. 1990. The Correlates of High Diversity in Lake Victoria Haplochromine Cichlids: a Neontological Perspective. In: Ross, R.M. & W.D. Ollmon (eds). *Causes of Evolution. A paleontological perspective.* University of Cicago Press, Chicago, London: 322-353.

Eccles, D.H. and E. Trewavas. 1989. *Malawian cichlid fishes. The classification of some Haplochromine genera.* Lake Fish Movies, Herten (W. Germany), 334 pages.

Fish, G.R. 1955. The food of *Tilapia* in East Africa. *Uganda Journal* 19: 85-89.

Fohrman, K. 1993a. Filtration. In: Konings, A. (ed). *Enjoying Cichlids.* Cichlid Press, St. Leon Rot: 25-30.

Fohrman, K. 1993b. Food and feeding. In: Konings, A. (ed). *Enjoying Cichlids.* Cichlid Press, St. Leon

Rot: 34-37.

Forsberg, L. 1993. The water. In: Konings, A. (ed). *Enjoying Cichlids.* Cichlid Press, St. Leon Rot: 19-24.

Fryer, G. 1961. Observations on the biology of the cichlid fish *Tilapia variabilis* Boulenger in northern waters of Lake Victoria (East Africa). *Revue Zool. Bot. afr.* 64: 1-33.

Fryer, G. and T.D. Iles. 1972. *The cichlid fishes of the Great Lakes of Africa: their biology and evolution.* Oliver and Boyd, London, 641 pages.

Goldschmidt, T. and K. Goudswaard. 1989. Reproductive strategies in haplochromines (Pisces, Cichlidae) from Lake Victoria. In: Goldschmidt, T. *An ecological and morphological fieldstudy on the haplochromine cichlid fishes (Pisces, Cichlidae) of Lake Victoria.* Ph.D. thesis, University of Leiden, Netherlands: 93-119.

Goldschmidt, T. and F. Witte. 1990. Reproductive strategies of zooplanktivorous haplochromine cichlids (Pisces) from Lake Victoria before the Nile perch boom. *Oikos* 58: 356-368.

Goldschmidt, T. and F. Witte. 1992. Explosive speciation and adaptive radiation of haplochromine cichlids from Lake Victoria: an illustration of the scientific value of a lost species flock. *Mitt. Internat. Verein. Limnol.* 23: 101-107.

Goldschmidt, T., F. Witte and J. de Visser. 1990. Ecological segregation in zooplanktivorous haplochromine species (Pisces, Cichlidae) from Lake Victoria. *Oikos* 58: 343-355.

Goldschmidt, T., F. Witte and J. Wanink. 1993. Cascading effects of the introduced Nile perch on the detritivorous/phytoplanktivorous species in the sublittoral areas of Lake Victoria. *Cons. Biol.* 7: 686-700.

Gophen, M., P.B.O. Ochumba and L.S. Kaufman. 1995. Some aspecte of perturbation in the structure and biodiversity of the ecosystem of Lake Victoria (East Africa). *Aquat. Living Resour.* 8: 27-41.

Goudswaard, K. and F. Witte. in press. The catfish fauna of Lake Victoria after the Nile perch upsurge. *Env. Biol. Fish.*

Graham, M. 1929. *The Victoria Nyanza and its Fisheries. A report on the fishing surveys of Lake Victoria*. London: Crown Agents for the Colonies, 256 pages.

Greenwood, P.H. 1956a. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae). Part I. *Bull. Br. Mus. nat. Hist.* (Zool.) 4: 223-244.

Greenwood, P.H. 1956b. The monotypic genera of cichlid fishes in Lake Victoria. *Bull. Br. Mus. nat. Hist.* (Zool.) 3: 295-333.

Greenwood, P.H. 1957. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae). Part II. *Bull. Br. Mus. nat. Hist.* (Zool.) 5: 73-97.

Greenwood, P.H. 1959a. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae). Part III. *Bull. Br. Mus. nat. Hist.* (Zool.) 5: 179-218.

Greenwood, P.H. 1959b. The monotypic genera of cichlid fishes in Lake Victoria. Part II. *Bull. Br. Mus. nat. Hist.* (Zool.) 5: 163-177.

Greenwood, P.H. 1960. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae). Part IV. *Bull. Br. Mus. nat. Hist.* (Zool.) 6: 227-281.

Greenwood, P.H. 1965. The cichlid fishes of Lake Nabugabo, Uganda. *Bull. Br. Mus. nat. Hist.* (Zool.) 12: 315-357.

Greenwood, P.H. 1966. Two new species of *Haplochromis* (Pisces, Cichlidae) from Lake Victoria. *Ann. Mag. nat. Hist.* 8: 303-318.

Greenwood, P.H. 1967. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae). Part VI. *Bull. Br. Mus. nat. Hist.* (Zool.) 15: 29-119.

Greenwood, P.H. 1973. A revision of the *Haplochromis* and related species (Pisces, Cichlidae) from Lake George, Uganda. *Bull. Br. Mus. nat. Hist.* (Zool.) 25: 139-242.

Greenwood, P.H. 1974. The cichlid fishes of Lake Victoria, East Africa: the biology and evolution of a species flock. *Bull. Br. Mus. nat. Hist.* (Zool.) Suppl 6: 1-134.

Greenwood, P.H. 1979. Towards a phyletic classification of the 'genus' *Haplochromis* (Pisces, Cichlidae) and related taxa. Part I. *Bull. Br. Mus. nat. Hist.* (Zool.) 35: 265-322.

Greenwood, P.H. 1980. Towards a phyletic classification of the 'genus' *Haplochromis* (Pisces, Cichlidae) and related taxa. Part II: the species from Lakes Victoria, Nabugabo, Edward, George and Kivu. *Bull. Br. Mus. nat. Hist.* (Zool.) 39: 1-101.

Greenwood, P.H. 1981. Species flocks and explosive evolution. In: Greenwood, P.H. and P.L. Forey (Eds). *Chance, Change and Challenge - The evolving biosphere*. Cambridge University Press & British Museum (Nat. Hist.), London: 61-74

Greenwood, P.H. 1983. On *Macropleurodus*, *Chilotilapia* (Teleostei, Cichlidae), and the interrelationships of African cichlid species flocks. *Bull. Br. Mus. nat. Hist.* (Zool.) 45: 209-231.

Greenwood, P.H. 1984. African cichlids and evolutionary theories. In: Echelle, A.A. and I. Kornfield

(Eds). *Evolution of Fish Species Flocks*. University of Maine at Orono Press, Orono, Maine: 141-154.

Greenwood, P.H. 1994. The species flock of cichlid fishes in Lake Victoria - and those of other African Great Lakes. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 44: 347-354.

Greenwood, P.H. and C.D.N. Barel. 1978. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae). Part VIII. *Bull. Br. Mus. nat. Hist.* (Zool.) 33: 141-192.

Harrison, K. 1991. The taxonomy of East African Nile perch, *Lates* spp. (Perciformes, Centropomidae). *J. Fish. Biol.* 38: 175-186.

Hecky, R.E. 1993. The eutrophication of Lake Victoria. *Verh. Int. Ver. Limnol.* 25: 39-48.

Hecky, R., F.W.B. Bugenyi, P.B.O. Ochumba, J.F. Talling, R. Mugidde, M. Gophen, L.S. Kaufman. 1994. Deoxygenation of the deep water of Lake Victoria, East Africa. *Limnol. Oceanogr.* 1476-1481.

HEST-Haplochromis Ecology Survey Team. 1989. Fish Stocks and Fisheries in Lake Victoria. A Handbook to the HEST/TAFIR,I & FAO/DANIDA, regional seminar, Mwanza, Jan.-Feb. 1989. *Report of the Haplochromis Ecology Survey Team (HEST) and the Tanzanian Fish. Res. Inst. (TAFIRI)* 53, Leiden, Netherlands.

Hilgendorf, F.M. 1988. Fische aus dem Victoria-Nyanza (Ukerewe See) gesammelt von dem verstorbenen Dr. G.A. Fischer. *Sber. Ges. naturf. Freunde Berl.*: 75-79.

Holzberg, S. 1978. A field and laboratory study of the behaviour and ecology of *Pseudotropheus zebra* (Boulenger), an endemic cichlid of Lake Malawi (Pisces: Cichlidae). *Z. Zool. Syst. Evol.-forsch.* 16: 171-187.

Hoogerhoud, R.J.C. 1984. A taxonomic reconsideration of the haplochromine genera *Gaurochromis* Greenwood, 1980 and *Labrochromis* Regan, 1920 (Pisces, Cichlidae). *Neth. J. Zool.* 34: 539-565.

Hoogerhoud, R.J.C., F. Witte and C.D.N. Barel. 1983. The ecological differentiation of two closely resembling *Haplochromis* species from Lake Victoria (*H. iris* and *H. hiatus*; Pisces, Cichlidae). *Neth. J. Zool.* 33: 283-305.

Katunzi, E.F.B. 1980. *Food preferences of four haplochromine cichlids from Mwanza Gulf in Lake Victoria*. M.Sc. thesis, University of Dar es Salaam, 132 pages.

Kaufman, L. in press. Asynchronous taxon cycles in haplochromine fishes of the greater Lake Victoria region. *S. Afr. J. Zool.*

Kaufman, L. and P. Ochumba. 1993. Evolutionary and Conservation Biology of Cichlid Fishes as Revealed by Faunal Remnants in Northern Lake Victoria. *Cons. Biol.* 7: 719-730.

Kaufman, L. and O. Seehausen. 1995. Cichliden von der ugandischen und der kenianischen Viktoriaseeküste. In: Stawikowski, R. (ed). *Cichliden. Festschrift zum 25jährigen Jubiläum der DCG*: 147-151.

Kirner, S. 1994. Neu importiert: Cichliden aus dem Viktoriasee. *D. Aqu. u. Terr. Z.* 47: 347-348.

Konings, A. 1988. *Tanganyika Cichlids.* Lake Fish Movies & Verduijn Cichlids, Herten (Germany) & Zevenhuizen (Netherlands), 272 pages.

Konings, A. 1995. *Malawi Cichlids in their Natural Environment.* Cichlid Press, St. Leon Rot (Germany), 352 pages.

Kudhongania, A.W. & A.J. Cordone. 1974a. Bathospatial distribution patterns and biomass estimates of the major demersal fishes in Lake Victoria. *Afr. J. Trop. Hydrobiol. Fish* 3: 15-31.

Lehman, J.T. and D.K. Branstrator. 1993. Effects of nutrients and grazing on the phytoplankton of Lake Victoria. *Verh. Int. Ver. Limnol.* 25: 850-855.

Liem, K.F. 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *Am. Zool.* 20: 295-314.

Lippitsch, E. 1993. A phyletic study on haplochromine fishes (Perciformes, Cichlidae) of East Africa, based on scale and squamation characters. *J. Fish. Biol.* 42: 903-946.

Lowe-McConnell 1956. Observations on the biology of *Tilapia* (Pisces, Cichlidae) in Lake Victoria, East Africa. *EAFFRO Suppl. Publ.* 1:1-72.

Marsh, A.C., A.J. Ribbink and B.A. Marsh. 1981. Sibling species complexes in sympatric populations of *Petrotilapia* Trewavas (Cichlidae, Lake Malawi). *Zool J. Linn. Soc.* 71: 253-264.

Maynard-Smith, J. 1966. Sympatric speciation. *American Naturalist* 100: 637-650.

Mayr, E. 1942. *Systematics and the Origin of Species.* Columbia University Press, New York.

McKaye, K.R. and W.M. Gray. 1984. Extrinsic barriers to gene flow in rock-dwelling cichlids of Lake Malawi: macrohabitat heterogeneity and reef colonization. In: Echelle, A.A. and I. Kornfield (Eds). *Evolution of Fish Species Flocks*. University of Maine at Orono Press, Orono, Maine: 169.183.

Meyer, A. 1993. Phylogenetic relationships and evolutionary processes in African cichlids. *Trends Ecol.*

Evol. 8: 279-284.

Meyer, A., T.D. Kocher, P. Basasibwaki & A.C. Wilson. 1990. Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondrial DNA sequences. *Nature* 347: 550-553.

Meyer, A., C. Montero and A. Spreinat. Evolutionary history of the cichlid fish species flocks of the East African great lakes inferred from molecular phylogenetic data. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* 44: 407-423.

Mugidde, R. 1993. The increase in phytoplankton primary productivity and biomass in Lake Victoria (Uganda). *Verh. Int. Ver. Limnol.* 25: 846-849.

Ochumba, P.B.O. 1987. Periodic massive fish kills in the Kenyan part of Lake Victoria. *Wat. Qual. Bull.* 12: 119-122.

Ochumba, P.B.O. and D.I. Kibaara. 1989. Observations on blue-green algal blooms in the open waters of Lake Victoria, Kenya. *Afr. J. Ecol.* 27: 23-24.

Oguto-Ohwayo, R. 1990. The decline of the native fishes of lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, *Lates niloticus*, and the Nile tilapia, *Oreochromis niloticus*. *Env. Biol. Fish.* 27: 81-96.

Oijen, M.J.P. van. 1978. The live coloration of certain previously described *Haplochromis* species. Appendix to: Greenwood, P.H. and C.D.N. Barel. A revision of the Lake Victoria *Haplochromis* species (Pisces, Cichlidae). Part VIII. *Bull. Br. Mus. nat. Hist.* (Zool.) 33: 141-192.

Oijen, M.J.P. van. 1982. Ecological differentiation among the haplochromine piscivorous species of Lake Victoria. *Neth. J. Zool.* 32: 336-363.

Oijen, M.J.P. van. 1989. Notes on the relationship between prey size and pharyngeal jaw size in piscivorous haplochromine cichlids from Lake Victoria. *Ann. Mus. Roy. Afr. Centr. Sc. Zool.* 257: 73-76.

Oijen, M.J.P. van. 1991. A systematic revision of the piscivorous haplochromine Cichlidae (Pisces: Teleostei) of Lake Victoria (East Africa). Part I. *Zool. Verh. Leiden* 272: 1-95.

Oijen, M.J.P. van. 1992. *Haplochromis howesi* spec. nov., a crab and fish eating cichlid from Lake Victoria. *Zool. Med. Leiden* 66: 561-597.

Oijen, M.J.P. van. 1995. The generic classification of the haplochromine cichlids of Lake Victoria, East Africa. *Zool. Verh. Leiden* 302: 57-110.

Oijen, M.J.P., F. Witte and E.L.M. Witte-Maas. 1981. An introduction to ecological and taxonomic investigations on the haplochromine cichlids from the Mwanza Gulf of Lake Victoria. *Neth. J. Zool.* 31: 149-174.

Oijen, M.J.P. and F. Witte. 1996. Taxonomical and ecological description of a species complex of zooplanktivorous and insectivorous cichlids from lake Victoria. *Zool. Verh. Leiden* 302: 1-56.

Owen, R.B., R. Crossley, T.C. Johnson, D. Tweddle, I. Kornfield, S. Davison, D.H. Eccles and D.E. Engstrom. 1990. Major low levels of Lake Malawi and their implications for speciation rates in cichlid fishes. *Proc. R. Soc. Lond. B* 240: 519-553.

Paterson, H.E.H. 1978. More evidence against speciation by reinforcement. *S. Afr. J. Sci.* 74: 369-371.

Piper, B.S., D.T. Plinston and J.V. Sutcliffe. 1986. The water balance of Lake Victoria. *Hydrological Sciences Journal* 31: 25-38.

Raymond, M. 1995. Victorian Secrets. *Trop. Fish. Hobb.* 43 (8): 16-28.

Regan, C.T. 1922. The cichlid fishes of Lake Victoria. *Proc. Zool. Soc. Lond.* (1922) 157-191.

Ribbink, A.J. 1991. Distribution and ecology of the cichlids of the African Great Lakes. In: Keeleyside, M.H.A. (ed). *Cichlid Fishes, Behaviour, Ecology, and Evolution*. Chapman and Hall: 36-59

Ribbink, A.J. and D.H. Eccles. 1988. Fish communities in the East African Great Lakes. In: Léveque, C., M.N. Bruton and G.W. Sentongo (eds). *Biology and ecology of African freshwater fishes*. Orstom, Paris: 277-300.

Ribbink, A.J., B.A. Marsh, A.C. Marsh, A.C. Ribbink and B.J. Sharp. 1983. A preliminary survey of the cichlid fishes of rocky habitats in Lake Malawi. *S. Afr. J. Zool.* 18: 149-310.

Sage, R.D., P.V. Loiselle, P. Basasibwaki and A.C. Wilson. 1984. Molecular versus morphological change among cichlid fishes of Lake Victoria. In: Echelle, A.A. and I. Kornfield (eds). *Evolution of Fish Species Flocks*. University of Maine at Orono Press, Orono, Maine: 185-201.

Schliewen, U.K., D. Tautz and S. Paäbo. 1994. Sympatric speciation suggested by monophyly of crater lake cichlids. *Nature* 368: 629-330.

Schraml, E. 1990. Haplochromisverwandte Buntbarsche aus Ostafrika. *D. Aqu. u. Terr. Z.* 43: 718-721.

Seehausen, O. 1992. Victorian Cichlids. Part I: Introduction to taxonomy and ecology. *The Cichlids Yearbook* 2: 54-59.

Seehausen, O. 1993a. *Foraging and spatial behaviour of rock dwelling cichlids in Lake Victoria in the light of competition, community structure, and speciation*. M.Sc. thesis, Universities of Hanover and Leiden, 234 pages.

Seehausen, O. 1993b. Victorian Cichlids. Part II: The oral shelling/crushing molluscivores. *The Cichlids Yearbook* 3: 50-55.

Seehausen, O. 1994. Victorian Cichlids. Part III: The epilithic algae scrapers. *The Cichlids Yearbook* 4: 42-51.

Seehausen, O. 1995a. The "Mbuna" of Lake Victoria. *Trop. Fish. Hobb.* 43 (8): 212-226.

Seehausen, O. 1995b. Die Felscichliden des Viktoriasees. *D. Aqu. u. Terr. Z.* 48: 190-196.

Seehausen, O. 1996a. A reconsideration of the ecological composition of the cichlid species flock in Lake Victoria before and after the Nile perch boom. In: van Densen, W. & R. Lowe-McConnell (eds). *Lacustrine Fish Communities in SE-Asia and Africa*. Samara Publishing Ltd., Cardigan, Dyfed, Great Britain.

Seehausen, O. 1996b. Distribution of, and reproductive isolation among colour morphs of a rock-dwelling Lake Victoria cichlid, *Haplochromis nyererei*. *Ecol. Freshw. Fish.* 5:

Seehausen, O. 1996c. A dynamic cichlid fauna as a complex indicator of environmental degradation in Lake Victoria. *Bull. Tanz. Fish. Res. Inst.* 2: in press.

Seehausen, O. 1996d. Fortpflanzungsverhalten felsbewohnender Viktoriaseecichliden in ihrem natürlichen Lebensraum. *D. Aqu. u. Terr. Z.* 49: 666-669.

Seehausen, O. and N. Bouton. 1996a. The community of rock-dwelling cichlids in Lake Victoria. *Bonner Zoologische Beitraege*: in press.

Seehausen, O. and N. Bouton. 1996b. Polychromatism in rock dwelling Lake Victoria cichlids: types, distribution, and observations on their genetics. *The Cichlids Yearbook* 6: 36-46.

Seehausen, O. and N. Bouton. in press. Microdistribution and temporal niche shifts in a rocky shore cichlid community in Lake Victoria. *Ecol. Freshw. Fish.*

Seehausen, O. and F. Witte. 1995. Extinction of many, survival of some. *Trop. Fish. Hobb.* 43 (7): 96-105.

Seehausen, O., N. Bouton, J.J.M. van Alphen and F. Witte. in press [a]. Feeding techniques, behavioural versatility and quantitative specialization of rock-dwelling haplochromine cichlids from Lake Victoria. *Oikos*.

Seehausen, O., F. Witte, E.F. Katunzi, J. Smits and N. Bouton. in press [b]. Patterns of the remnant cichlid fauna in southern Lake Victoria. *Conservation Biology.*

Seehausen, O., S. Kangwe and A. Samwel-Terry. 1996. Wasserhyazinthe und Fischerei bedrohen Viktoriasee-Cichliden. *D. Aqu. u. Terr. Z.* 49: 112-116.

Selbrink, B. 1985a. Viktoriasjöns ciklider, del 3: *Psammochromis riponianus*. *Akvariet* 59: 356-357.

Selbrink, B. 1985b. Viktoriasjöns ciklider, del 2: Silverpilen - *Prognathochromis spec. aff. longirostris*. *Akvariet* 59: 340-341.

Selbrink, B. 1986. Viktoriasjöns ciklider, del 6: *Neochromis nigricans* - en "mbuna" fran Viktoriasjön. *Akvariet* 60: 44-45.

Skúlason, S., D.L.G. Noakes and S.S. Snorrason. 1989. Ontogeny of trophic morphology in four sympatric morphs of Arctic charr *Salvelinus alpinus* in Thingvallavatn, Iceland. *Biol. J. Linn. Soc.* 38: 281-301.

Snoeks , J. 1988. Redescription d´*Haplochromis paucidens* Regan, 1921 et description d´*Haplochromis occultidens* sp.n. (Pisces, Cichlidae) du lac Kivu en Afrique. *Cybium* 12: 203-218.

Snoeks, J. 1994. The Haplochromines (Teleostei, Cichlidae) of Lake Kivu (East Africa). A taxonomic revision with notes on their ecology. *Ann. Mus. Roy. Afr. Centr., Sc. Zool.* 270: 1-221.

Stager, J.C., P.N. Reinthal and D.A. Livingstone. 1986. A 25,000-year history for Lake Victoria, East Africa, and some comments on its significance for the evolution of cichlid fishes. *Freshwat. Biol.* 16: 15-19

Stauffer, J.R. and K.R. McKaye. 1986. Description of a paedophagous deep-water cichlid (Teleostei: Cichlidae) from Lake Malawi, Africa. *Proc. Biol. Soc. Wash.* 99: 29-33.

Sturmbauer, C. and A. Meyer. 1993. Mitochondrial phylogeny of the endemic mouthbrooding lineages of cichlid fishes from Lake Tanganyika in eastern Africa. *Mol. Biol. Evol.* 10: 751-768.

Talling, J.F. 1957. Some observations on the stratification of Lake Victoria. *Limnol. Oceanogr.* 2: 213-221.

Talling , J.F. 1966. The annual cycle of stratification and phytoplankton growth in Lake Victoria (East Africa). *Int. Revue ges. Hydrobiol.* 51: 545-621.

Taylor, E.B. and P. Bentzen. 1993. Evidence for multiple origins and sympatric divergence of trophic ecotypes of smelt (*Osmerus*) in northeastern North

America. *Evolution* 47: 813-832.

Taylor, E.B. and J.D. McPhail. 1994. Molecular tests of speciation scenarios in sympatric sticklebacks, *Gasterosteus*. *Second International Symposium on Stickleback Behaviour*, Leiden/Netherlands, 28.08.-01.09.1994. Abstract.

Temple, P.H. 1967. Causes of intermittent decline in the level of Lake Victoria during the Late Pleistocene and Holocene. In: Steel, R.W. and R. Lawton (eds). *Liverpool essays in geography*: 43-63.

Trewavas, E. 1983. The tilapiine fishes of the genera *Sarotherodon*, *Oreochromis* and *Danakilia*. British Museum (Natural History) London, 583 pages.

Turner, G.F. and M.T. Burrows. 1995. A model of sympatric speciation by sexual selection. *Proc. R. Soc. Lond. B.* 260: 287-292.

Wanink, J.H. 1991. Survival in a perturbated environment: the effects of Nile perch introduction on the zooplanktivorous fish community in Lake Victoria. In: Ravera, O. (ed). *Terrestrial and aquatic ecosystems: perturbation and recovery.* Ellis Horwood Ltd., Chichester.

Wilhelm, W. 1980. The disputed feeding behaviour of a paedophagous haplochromine cichlid (Pisces) observed and discussed. *Behaviour* 74: 310-323.

Wilson, E.O. 1994. *The Diversity of Life*. Penguin Books Ltd., 406 pages.

Witte, F. 1984. Ecological differentiation in Lake Victoria haplochromines: comparison of cichlid species flocks in African lakes. In: Echelle, A.A. and I. Kornfield (eds). *Evolution of Fish Species Flocks*. University of Maine at Orono Press, Orono, Maine: 155-167.

Witte, F. & W.L.T. van Densen (eds). Fish Stocks and Fisheries of Lake Victoria. A handbook for field observations. Samara Publishing Ltd., Cardigan, Dyfed, Great Britain.

Witte, F., T. Goldschmidt, J. Wanink, M. van Oijen, K. Goudswaard, E. Witte-Maas and N. Bouton. 1992. The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. *Env. Biol. Fish.* 34: 1-28.

Witte, F., T. Goldschmidt and J. Wanink. 1995. Dynamics of the haplochromine cichlid fauna and other ecological changes in the Mwanza Gulf of Lake Victoria. In: Pitcher, T.J. and P.J.B. Hart (eds). *The Impact of Species Changes in African Lakes*. Chapman and Hall, London: 83-110.

Witte, F. and M.J.P. van Oijen. 1990. Taxonomy, ecology and fishery of haplochromine trophic groups. *Zool. Verh.* 262: 1-47.

Witte, F. and E.L.M. Witte-Maas 1987. Implications for taxonomy and functional morphology of intraspecific variation in haplochromine cichlids of Lake Victoria. In: Witte, F. *From Form to Fishery*. Ph.D. thesis, Leiden University, chapter II.

Witte-Maas, E.L.M. 1981. Eggsnatching: an observation on the feeding behaviour of *Haplochromis barbarae* Greenwood, 1967 (Pisces, Cichlidae). *Neth. J. Zool.* 31: 786-789.

Witte-Maas, E.L.M. and F. Witte. 1985. *Haplochromis nyererei, a new cichlid fish from Lake Victoria named in honour of Mwalimu Julius Nyerere, president of Tanzania.* Brill Publishers, Leiden, 13 pages.

Species Index

The index lists all cichlid species that are dealt with in the text and that are shown in photographs. Vertical bar and Chessboard *Mbipi* are sorted alphabetically within the species complexes. All other species are sorted alphabetically, their (sub)generic assignment fol-lowing the species name. Page numbers printed in boldface refer to illustrations. Page numbers in italics refer to distribution maps.

LAKE VICTORIA ROCK CICHLIDS

This is the first popular book about Lake Victoria cichlids, and it reports about a species assemblage that is largely new to aquarists and scientists alike. The 173 species discussed constitute a *Mbuna*-like species assemblage of Lake Victoria cichlids, that was previously believed not to exist! The "new" cichlid assemblage carries a great potential both for biological research and for the aquarium hobby. The purpose of this book is to give a first introduction to this newly discovered fauna, and to make researchers, hobbyists, and conservationists aware of its riches.

Most emphasis is laid upon the presentation of the various species complexes and species, with much new information about distribution, ecology, and behaviour in their natural environment. For this purpose underwater work using SCUBA was done for the first time in Lake Victoria.

High time therefore, to look at Lake Victoria's rock cichlids more carefully....

ISBN 90-800181-6-3