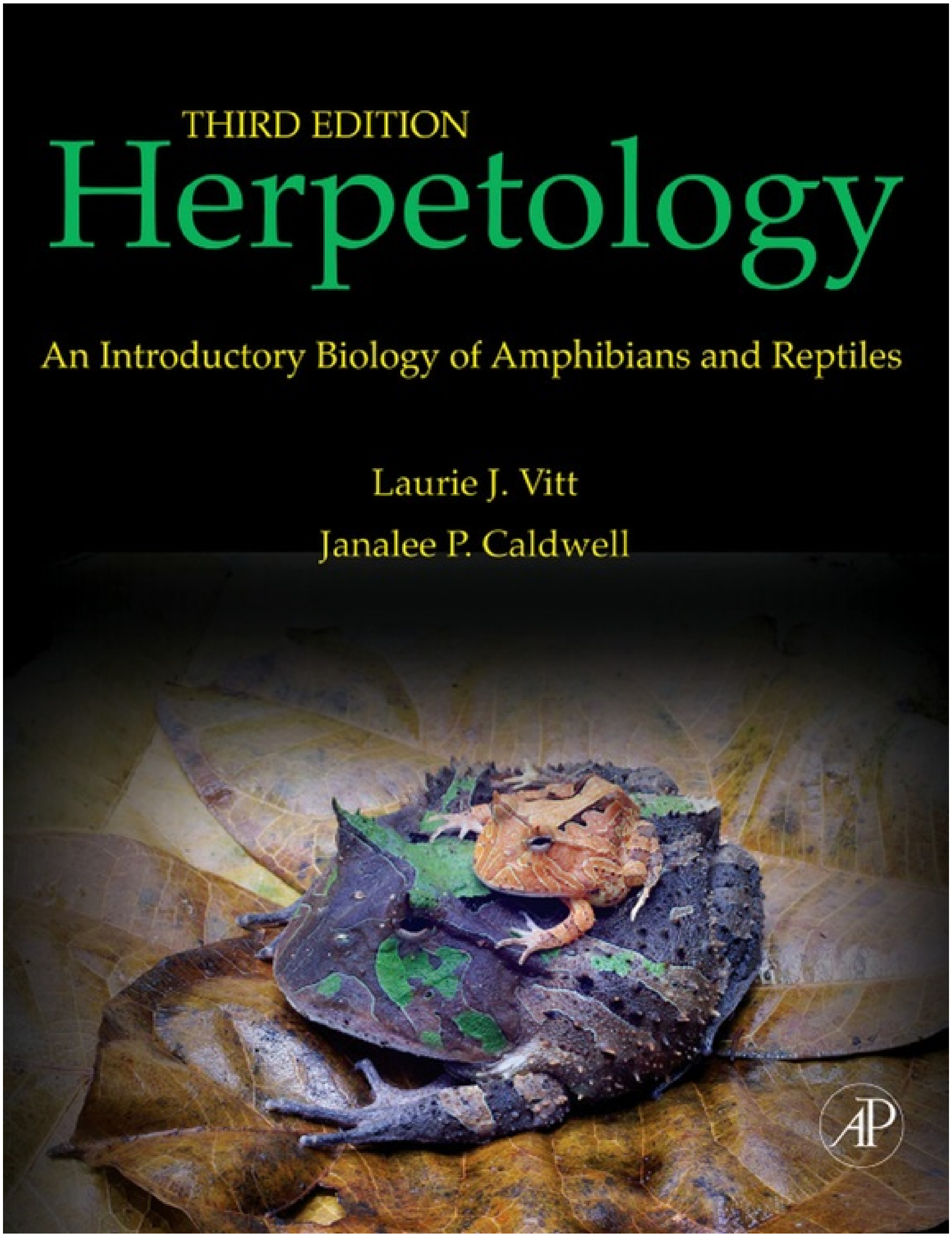
THIRD EDITION

Herpetology

An Introductory Biology of Amphibians and Reptiles

Laurie J. Vitt

Janalee P. Caldwell



Herpetology

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3rd Edition

Laurie J. Vitt and Janalee P. Caldwell

Sam Noble Oklahoma Museum of Natural History Department of Zoology

University of Oklahoma

Norman, Oklahoma

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Dedication

First and foremost, we dedicate this book to George entire series. Finally, we dedicate this book to all research-R. Zug, our former coauthor (see Herpetology: An Intro-ers, teachers, students, and amateurs who share a common ductory Biology of Amphibians and Reptiles, Second Edi-interest in amphibians and reptiles (even though these two tion), who, like us, had a vision of a herpetology textbook groups are not closely related phylogenetically), and who that would capture the interest of students who want to share the common goal of conserving these remarkable learn about what we consider to be the most fascinating organisms and their natural habitats.

organisms on Earth. We also dedicate this book to Cole-L. J. V. and J. P. C.

man and Olive Goin, pioneers in North American herpetology whose original herpetology textbook led to this

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Foreword

The diversity of living creatures on our planet is extraordi-and can even tell the difference between a crocodile and nary—and thus, trying to understand how those organisms a lizard. And it is a major reason why there is immense function, and how and why they do the things they do, is value in defining a scientific field based on evolutionary an awesome challenge. To make the challenge a bit more relatedness of the creatures being studied, not just on manageable, we traditionally divide the study of biology methods or concepts. So "herpetology" is a useful cate-into many categories, some based on methodology (e.g., gory: If we really want to understand what animals do, "microscopy" or "molecular biology"), some on function we can't ignore the history behind each type of organism.

(e.g., "ecology" or "physiology"), and some on relatedness Many of its features will be determined by that history, not among the things that are to be studied (e.g., "ornithology"

by current forces. Because of that historical underpinning, or "herpetology").

At first sight, this last way of slicing the most effective way to answer general questions in the cake seems a bit old-fashioned—surely we can simply biology may be to work within one or more of those ask the same questions and use the same methods, regard-major branches in the tree of life. Starting from common less of what kind of organism we might be studying? If so, ancestors, we can see with much greater clarity how evo-are traditional taxonomy-based divisions just historical lutionary forces have created rapid change in some cases relics of the early naturalists, doomed to eventual extinc-

(why are chameleons so incredibly weird compared with tion by the rise of powerful conceptual and methodologi-other lizards?), have produced remarkably little change cal advances?

over vast timescales in others (can it really be true that Nothing could be further from the truth. Entrancing as crocodiles are more closely related to birds than to the new approaches and conceptual divisions are, the real-lizards?), and have even generated convergent solutions ity of life on Earth is that organisms do fall into instantly in distantly related species exposed to similar adaptive recognizable types. Few people would mistake a tree for a challenges (like horned lizards in the deserts of North lizard, or a whale for an insect. The reason is simple: Evo-America compared with thorny devils in the deserts of lution is an historical process that creates biodiversity by Australia).

the accumulation of small changes along genealogies, with Allied to the greater clarity that comes from comparing the vast majority of species becoming extinct during that like to like, and including genealogy in our thinking, are process. So the end result at any time in Earth's history other great advantages to taxon-based categories like "heris a series of terminal branches from the great tree of petology." Organisms are composites of many traits, and life—terminal branches that form larger branches, that in these need to work together for the creature to function turn coalesce to form even larger branches, and so forth.

effectively. So we can't really look at metabolic rate sep-All the species within each of those larger branches share arately from foraging behavior, or social systems sepa-common ancestors not shared by any species on the other rately from rates of water loss. Biology forges functional branches, and as a result, the species within each branch links between systems that our conceptual and methodo-resemble each other in many ways. For example, no logical classification systems would treat in isolation from amphibian embryo grows up with an amniotic membrane each other, ignoring their need for integration within a around it in the egg, whereas every reptile embryo has functioning individual. And there are many other advan-one.

tages also. In a purely pragmatic sense, the methods that The evolutionary conservatism of major characteristics we use to study animals—such as the ways we observe such as metabolic rates, reproductive modes, feeding them, catch them, handle them, mark them, and follow structures, and the like in turn have imposed evolutionary them around—depend enormously on many of the traits pressures on myriad other features—and the end result is that differ so conspicuously between major vertebrate that the diversity of life is packaged into a meaningful lineages. A textbook of herpetology can thus teach us set of categories. That is the reason why most of us can more about how to study these animals than can a text-easily distinguish a frog from any other kind of animal book focused on any single functional topic. And lastly, ix

the conservation challenges facing reptiles and amphibians captures the excitement of herpetology and will do much also are massively affected by their small body sizes, low to instill that appreciation.

rates of energy use, primarily tropical distributions, and Rick Shine

the like—so that if we are to preserve these magnificent School of Biological Sciences

animals for future generations, we need a new generation University of Sydney

of biologists who can comprehend the sophisticated func-Sydney, Australia tioning of these threatened creatures. This marvelous book

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Introduction

obvious reasons. Amphibians (frogs in particular) have It is an admirable feature of herpetologists that they are able to gained enormous popularity in the arts and crafts trade, cross the boundaries between different aspects of their subject, partly because they are colorful and diverse, and partly which remains, perhaps more than other branches of zoology, a because they are nonthreatening. The pet trade has brought single coherent discipline.

amphibians and reptiles into the homes of millions of peo-A. d'A. Bellairs and C. B. Cox, 1976.

ple and sparked their interest in these remarkable animals.

It is our hope that we can use that interest to draw students In 2001, we joined George R. Zug to publish the second edi-into understanding general biological concepts, all of tion of his highly successful textbook, Herpetology: An which apply to the biodiversity surrounding us that helps Introductory Biology of Amphibians and Reptiles. For us, sustain life on Earth.

and for George, it was an exciting collaboration, and we Our primary goals in revising Herpetology: An Intro-fueled each other's interest and enthusiasm as we worked ductory Biology of Amphibians and Reptiles are to (1) together on the book. George made it clear at the time that update the text to reflect some of the truly exciting discov-the second edition would be his last involvement in the text-eries that have been made since about 2000 when we com-book, not because he had lost interest (herpetologists never pleted the second edition, published in 2001; (2) update lose interest!), but rather because he was at a point in his the taxonomy, which in some cases has changed radically career where he had other goals to accomplish.

as the result of much more sophisticated evolutionary ana-Herpetology is a rapidly evolving field, and although it lyses (e.g., anurans); and (3) introduce the reader to some is a taxonomically delimited field, research on amphibians of the leading herpetological researchers by featuring their and reptiles has set new directions, defined new fields, and work throughout the book. In doing the latter, we empha-led to major discoveries in all conceptual areas of biol-size that many truly phenomenal researchers make major ogy—discoveries that have changed the way we think discoveries every day—we have selected a few from the about life on Earth. We know more now than we ever many, and with future editions, our selections will vary.

did, and we will continue to know and understand more Our intent is not to slight any researcher by noninclusion as innovative technologies allow us to explore new ideas but rather to highlight a few of the many in an attempt in ways never before thought possible. At the same time, to make research discovery a little more personal. After we are losing species and habitats at a rate unparalleled all, successful herpetologists are really just normal people in the history of life, and much of it can be tied directly driven by their interest in herpetology, just as rock stars to human activity and indirectly to human population are normal people driven by their interest in music and growth. When Coleman and Olive Goin published Intro-the performing arts.

duction to Herpetology in 1962, population of the Earth We have explicitly tried to keep the text at a level that was nearly 3 billion; when George Zug published the first will be of use to undergraduates with only a basic back-edition of Herpetology: An Introductory Biology of ground in biology, as well as those with a much broader Amphibians and Reptiles in 1993, the population was 5.4

background. We have added color throughout the text, billion; today, the world population approaches 7 billion!

which we believe aids significantly in showcasing how Not only has the world population reached an unprece-special these animals are. Color is also very useful in dented high, but the exponential rate of population chapters in which we discuss crypsis, aposomatic colora-increase is reflected in the exponential increase in environ-tion, and social behaviors mediated by visual displays.

mental effects. We consider it imperative that students We remind the reader that not only are amphibians and understand the basis for life around them and the connec-reptiles part of our own evolutionary history, but they also tions between our survival and the survival of other spe-are an integral part of our natural heritage. They, along cies. The biology of amphibians and reptiles provides a with all other animal and plant species, compose life on unique opportunity to achieve that goal, for several rather Earth.

Introduction

Classification and nomenclature continue to change, evolutionary time period (e.g., not only are different and if anything, the rate of change is greater period (e.g., not only are different and if anything, the rate of change is greater than it ever "families" different ages, they also are nested within each has been. New fossils, new techniques for obtaining and other). We have attempted to be as current as possible, and interpreting phylogenetic data, and the beginnings of a our classification sections reflect published interpretations truly phylogenetic taxonomy and its associated nomencla-through December 2007. Numerous phylogenetic hypoth-ture are changing amphibian and reptilian classification eses exist for most groups of amphibians and reptiles, monthly. The ability to recover relationships among taxa resulting in different classifications, sometimes strikingly at all levels based on combinations of morphological, gene different. We have selected a single cladistic interpretation sequence, behavioral, physiological, and ecological data for each group or combined the results of two interpreta-

(total evidence) demonstrates the complexity of the evolu-tions when a single cladistic analysis for all members of tionary history of amphibians and reptiles. At the same the group (clade) was not available. We discuss other time, it brings us much closer to constructing phylogenetic interpretations and analyses, but not necessarily all avail-hypotheses that accurately reflect relationships. Most able studies, to ensure that readers are aware that other striking is the observation that classical Linnean taxonomy interpretations exist. We use Latinized familial and subfa-presents a false impression about relationships of taxa. For milial group names for monophyletic groups and Angli-example, Linnean taxonomy implies that all families are cized or Latinized names in quotes for groups that are of equal age, that all orders are equal age, and so on.

uncertain monophyly. Some authors have not assigned Although some elements of Linnean taxonomy are useful family names to some species and groups of species that in allowing us to talk about amphibians and reptiles, the represent a sister taxon to another family; where Latinized basic notion that organisms can be placed in arbitrary familial names are available, we have used the available groups and given names is highly misleading. Our classifi-name or elevated a subfamilial name if that latter taxon cation contains a mix of lower-taxonomic-level Linnean includes the same set of species. Distributions are an taxonomy (to facilitate discussion) and phylogenetic tax-important component of an organism's biology; our maps onomy (to reflect relationships).We use species, genus, show the natural (nonhuman dispersed) distribution as best subfamily, and family as labels, emphasizing that each we were able to determine it.

does not correspond to a given phylogenetic distance or

Part I

Evolutionary History

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Chapter 1

Tetrapod Relationships

and Evolutionary Systematics

Amphibians and Reptiles—

Evolution of Early Amniotes

Systematic Analysis

Evolutionary History

Early Tetrapods and Terrestriality

Methods of Analysis

Relationships Among Vertebrates

Early Amniotes

Numeric Analyses

Origin of Tetrapods

Radiation of Diapsids

Phylogenetic Analyses

Major Features of Early Tetrapod

Linnean Versus Evolutionary

Questions

Evolution

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Evolution of Early Anamniotes

Rules and Practice

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Ancient Amphibians

Evolution-Based Taxonomy

Modern Amphibians—The

Systematics—Theory and Practice

Lissamphibia

Herpetology is the study of amphibians and reptiles. Living Amphibians and reptiles (collectively, herps) are not amphibians and reptiles are representatives of a small num-each other’s closest relatives evolutionarily, yet they ber of the many historical tetrapod radiations (Table 1.1; have traditionally been treated as though they are related Fig. 1.1). Amphibians were the first truly terrestrial verte-

(e.g., “herpetology” does not include birds and mammals).

brates. Their ancestors were lobe-finned fishes (Sarcoptery-Nevertheless, many aspects of the lives and biology of gii), a group of bony fishes (Osteichtyes). These fishes amphibians and reptiles are complementary and allow appeared in the Devonian Period (more than 380 million zoologists to study them together using the same or similar years before present [mybp]) and radiated in fresh and techniques. Biological similarities between amphibians and salt water. The earliest fossils assigned to Tetrapoda (from reptiles and the ease of field and laboratory manipulation of Greek, tetra = four, poda = foot) included Acanthostega many species have made them model animals for the study and Ichthyostega, both of which were completely aquatic of ecology. Amphibians and reptiles have played promi-but had four distinct limbs. They appeared in the late Devonent roles in research on ecology (e.g., tadpoles, salaman-nian (about 360 mybp) and are in a group of tetrapods der larvae, lizards, the turtle Trachemys scripta), behavior referred to as ichthyostegalians (Fig. 1.1). Amphibians have (e.g., the frogs Engystomops [Physalaemus] and Lithobates successfully exploited most terrestrial environments while [Rana] catesbeianus), phylogeography (e.g., the lizard remaining closely tied to water or moist microhabitats for genus Crotaphytus, plethodontid salamanders), genetics reproduction. Most amphibians experience rapid desicca-

(Xenopus), developmental biology (e.g., Xenopus, pletho-tion in dry environments, but some species have evolved dontid salamanders, reptiles), viviparity (squamates), and spectacular adaptations that permit existence in extreme evolutionary biology (e.g., Anolis, Lepidodactylus).

habitats.

During the Carboniferous, about 320 mybp, the anthracosaurs appeared (Fig. 1.1). They not only were able to AMPHIBIANS AND REPTILES— reproduce on land in the absence of water but also had an EVOLUTIONARY HISTORY

effective skin barrier that presumably reduced rapid and excessive water loss. Extant reptiles (including birds) and Living amphibians are represented by three clades: Gym-mammals descended from anthracosaurs. The study of birds nophiona (caecilians), Caudata (salamanders), and Anura and mammals, formally called Ornithology and Mammal-

(frogs) (Table 1.2). Detailed characterizations and taxon-ogy, respectively, are beyond the scope of this book.

omy of living amphibians and reptiles are given in Herpetology, 3rd Ed.

(tuataras and squamates) (Table 1.2). Until recently, TABLE 1.1 A Hierarchial Classification of turtles were considered as the outgroup to all other reptiles Vertebrates Showing the Position of the Tetrapoda because their skulls have no fenestre (openings), which and Its Subgroups as Members of the Bony Fish placed them with the anapsids, an extinct and very old Clade.

group of reptiles. Recent nuclear DNA data indicate that their "anapsid" skull condition may be derived from a Vertebrata diapsid skull and thus they belong in with crocodilians Gnathostomata—jawed vertebrates

Osteichthyes (Teleostomi)—bony fishes

and birds. Turtles, like frogs, cannot be mistaken for Actinopterygii—rayfinned fishes

any other animal (Fig. 1.3). The body is encased within Teleostei

upper and lower bony shells (carapace and plastron, Sarcopterygii—fleshy-finned fishes

respectively). In some species, the upper and lower shells Coelacanthiformes (Actinistia)—coelacanths fit tightly together, completely protecting the limbs and Dipnoi—lungfishes

head. Although turtles are only moderately speciose, they Ostelepiformes—Eusthenopteron and relatives are ecologically diverse, with some fully aquatic (except Porolepiformes

for egg deposition) and others fully terrestrial. Some are Tetrapoda—tetrapods

Ichthyostegalia—Ichthyostega and relatives tiny in size whereas others are gigantic, and some are her-Amphibia—amphibians bivores and others are carnivores. Other living archosaurs Colosteidae—Greererpeton and relatives

include the closely related crocodilians and birds. Birds Temnospondyli—temnospondyls

are reptiles because they originated within Archosauria, Lissamphibia—extant amphibians

but they have traditionally been treated as a separate group Anthracosauria—anthracosaurs

of vertebrates. Crocodilians are predaceous, semiaquatic Amniota—amniotes

reptiles that swim with strong undulatory strokes of a Reptilia (Sauropsida)—reptiles

powerful tail and are armored by thick epidermal plates Synapsida—synapsids

underlain dorsally by bone. The head, body, and tail are Note: The origin of the tetrapods among the sarcopterygians is presented as unresolved.

elongate, and the limbs are short and strong. The limbs Category titles are not assigned to the hierarchical ranks, and some ranks or nodes are allow mobility on land, although terrestrial activities are absent. Alternate group names are in parentheses; these alternates are nearly equivalent but not identical in taxa content. Differences between this classification and that usually limited to basking and nesting.

derived from Fig. 1.1 result from a combination of different sets of taxa, characters, and Tuataras and the squamates comprise the Lepidosauria.

analyses.

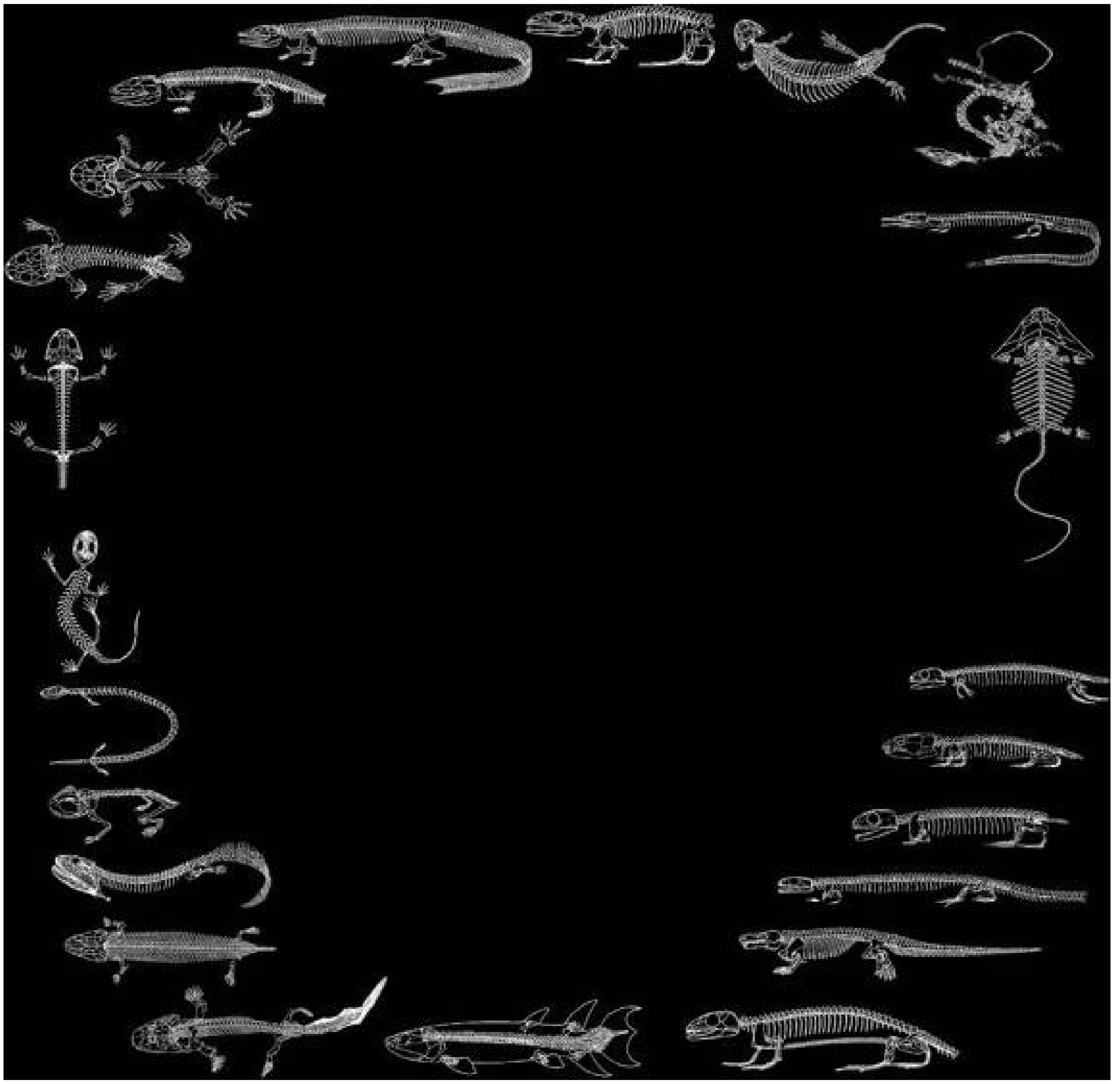
Represented by only two species on islands off the coast of New Zealand, the lizard-like tuataras diverged early within the lepidosaurian clade (Fig. 1.3). Lizards, snakes, and amphisbaenians comprise the Squamata. These three Part VII. Caecilians superficially resemble earthworms groups are easily recognized and, as a result, are often trea-

(Fig. 1.2). All extant caecilians lack limbs, are strongly annu-ted in popular literature and field guides as though they are lated, and have wedge-shaped, heavily ossified heads and sister taxa or at least equal-rank clades. They are not.

blunt tails. This morphology reflects the burrowing lifestyle Snakes and amphisbaenians are nested within lizards (see of these tropical amphibians. Salamanders have cylindrical Chapters 20 and 21). Squamates are the most diverse and bodies, long tails, distinct heads and necks, and well-devel-speciose of living reptiles, occupying habitats ranging from oped limbs, although a few salamanders have greatly reduced tropical oceans to temperate mountaintops. Body forms and limbs or even have lost the hindlimbs (Fig. 1.2). Salamanders sizes vary considerably. Most are terrestrial or arboreal, are ecologically diverse: Some are totally aquatic, some bur-though many snakes are semiaquatic, spending much of row, many are terrestrial, and many others are arboreal, living their lives in or immediately adjacent to freshwater, or, less in epiphytes in forest canopy. Frogs are unlike other verte-commonly, in estuaries and seawater. The term “lizard” is brates in having robust, tailless bodies with a continuous head usually used to refer to all squamates that are not snakes and body and well-developed limbs (Fig. 1.2). The hindlimbs or amphisbaenians. Thus “lizards” are highly variable mor-typically are nearly twice the length of the body, and their phologically and ecologically, but most have four well-morphology reflects their bipedal saltatory locomotion. Not developed limbs and an elongate tail. Amphisbaenians are all frogs jump or even hop; some are totally aquatic and use elongate with short, stubby tails, scales arranged in rings a synchronous hindlimb kick for propulsion, whereas others around the body, and mostly limbless (the exception is simply walk in their terrestrial and arboreal habitats. Among Bipes, which has two mole-like front limbs). They are sub-amphibians, frogs are the most speciose and widely terranean. They are a monophyletic group of lizards.

distributed group; in addition, they are morphologically, Snakes are the most speciose of several groups of limbless physiologically, and ecologically diverse.

or reduced-limbed lizards. A few snakes are totally aquatic Living reptiles are represented by the clades Archo-and some are even totally subterranean. Like amphisbae-sauria (turtles, crocodilians, and birds), and Lepidosauria nians, snakes are a monophyletic group of lizards.



Seymouria baylorensis / sanjuanensis

Pholiderpeton scuti

Gephyrostegus bohemicus

Solenodonsaurus janenschi

Anthracosaurus russelli

Bruktererpeton fiebigi

Proterogyrinus scheelei

Pholiderpeton

Archeria crassidisca

Discosauriscus austriacus

Eoher

Eucritta melanolimnetes

Caerorhachis bairdi

Coch

Kotlassia prima

peton watsoni

Phlegethontia linearis

Oestocephalus amphiuminum

leosaurus florensis

Chenoprosopus lewisi

attheyi

gerum

Lethiscus stocki

Sauropleura pectinata / scalaris

Trimerorhachis insignis

Ptyonius marshii

Edops craigi

Neldasaurus wrightae

Uroc

ordylus wand esfordii

Isodectes obtusus

Scincosaur

Balanerpeton

Dendrerpeton acadianum

Ker

us crassus

Bat

aterpeton gal

rachiderpeton reticulatum

woodi

Eryops megacephalus

vani

Diceratosaurus brevirostr

Ache

loma cumminsi

Dipocaulus magnicor

Phonerpeton pricei

is

Dipoc

nis

Ecolsonia cutlerensis

eraspis burkei

Acherontisc

Broil

Microsaurs

us caledon

ius brevis

iae

Schoenfelderpeton prescheri

Lepospondyls

Adelospondylus watsoni

Anthracosaurs

Anthracosaurs

Adelogyrinus symorhynchus

Leptorophus tener

Temnospondyls

Ichthyostegalians

Dolichopareias disjectus

Apateon pedestris

ryi

Brachydectes elongatus / newber

Micromelerpeton credneri

ikani

Microbrachis pel

Eoscopus lockardi

are

yelli

Platyrhinops l

Odonterpeton triangul

ion longicostatum

ns

Hyloples

Amphibamus grandiceps

petes fritschia

AE

Batro

Doleserpeton annecte

a

RPETONTID

Tuditanus punctulatus

ALBANE

ia micropod

Pantylus cordatus

Eocaecil

itzi

Valdotriton gracilis

Stegotretus agyrus

Karaurus sharovi

Asaphestera intermedia

Saxonerpeton gein

Triadobatrachus massinoti

Hapsidopareion lepton

Baphetes kirkbyi

rnbergi

tis elongatum

Micraroter erythogeios

Whatcheeria deltae

ari

Megalocephalus pachycephalus

nn

Pelodoso

Rhynchonkos stovalli

Crassigyrinus scoticus

Euryodus primus

ga gu

Colosteus scutellatus

Tulerpeton curtum

Westiothiana lizziae

Diadectes absitus

Cardiocephalus ste

Greererpeton burkemorani

Captorhinus aguti

Limnoscelis paludis

Ichthyostega stensioeiAcanthoste

Ventastega curonica

Paleothyris acadiana

Eusthenopteron foordi

Panderichthys rhombolepis

Petrolacosaurus kansensis

FIGURE 1.1 A super-tree of relationships among early (fossil) tetrapods. To aid in interpreting the structure of the tree, we have color-coded major groups that are discussed in the text. In addition, color-coded lines indicate clades from which extant ampibians (orange) and extant reptiles (red and blue) arose. Orange lines indicate the Lissamphibia, the group from which all extant amphibians originated. Blue lines indicate the Parareptilia, the group from which turtles were once believed to have originated. Although modern turtles have historically been placed in the Parareptilia based on their anapsid skull, recent molecular data indicate that they are nested within the Eureptilia. Red lines indicate the Eureptilia, the group from which all modern reptiles originated.

It is useful to refer back to this graphic as you read through the history of tetrapod evolution in order to tie group or fossil names with appropriate evolutionary groups. Adapted from Ruta and Coates, 2003, and Ruta et al., 2003.

RELATIONSHIPS AMONG VERTEBRATES

Origin of Tetrapods

history of life, ultimately allowing vertebrates to invade nearly all of Earth’s terrestrial environments. Understand-The transition from fish to tetrapod set the stage for one ing the complexity of the early evolutionary history of tet-of the most spectacular radiations in the evolutionary rapods has been a challenge for paleontologists because

discarding the original idea that tetrapods evolved from TABLE 1.2 A Hierarchical Classification for Living lobe-finned fishes (sarcopterygians) that were forced Amphibians and Reptiles.

onto land because of major droughts during the Devonian. The idea was that only those fish that could evolve Tetrapoda

limbs

for terrestrial

movement on

land

survived.

Amphibia

Microsauria

Although various scientists challenged this idea, it was Temnospondylia

not until the discovery of well-preserved material of Lissamphibia

Acanthostega in the late 1980s that a new paradigm of Gymnophiona—caecilians

tetrapod evolution became widely accepted. Acanthos-Caudata—salamanders tega was clearly a tetrapod but was not a land animal.

Anura—frogs

It had four limbs with digits, but no wrists and could Anthracosauria

not have supported itself on land. This realization and a Amniota

reinterpretation of Ichthyostega as a fish with limbs led Synapsida

Reptilia

to the currently accepted idea that tetrapod limbs func-Parareptilia tioned for locomotion in shallow, vegetated Devonian Eureptilia

swamps. Only later did their descendants emerge onto Diapsida

land.

Sauria

An increase in exploration of Devonian sites has Archosauria

provided new material in recent years, and a much clearer Testudines—turtles

picture of the evolution of this group is emerging Crocodylia—crocodylians

(Fig. 1.1). To date, 17 distinct Devonian tetrapods from Aves—birds

Lepidosauria

nine localities worldwide have been discovered, and Sphenodontia—tuataras

12 genera have been described. Other significant discov-Squamata—lizards (including eries include several new proto-tetrapods and other tetra-amphisbaenians and snakes pods from the Early Carboniferous. The localities and named tetrapod genera include Pennsylvania (Hynerpeton, Sources: Carroll, 2007; Gauthier et al., 1988a, 1989.

Densignathus);

Scotland

(Elginerpeton);

Greenland

(Ichythostega, Acanthostega); Latvia (Obruchevichthys, Ventastega); Tula, Russia (Tulerpeton); Livny, Russia (Jakubsonia); New South Wales (Metaxygnathus); China (Sinostega); and Canada (Tiktaalik). Most early tetrapods many fossil taxa are represented only by fragments of are known from Euramerica, where, in Late Devonian, this jaws or limbs, making it difficult to determine phyloge-land mass was separate from Gondwana. Two species, netic relationships. To help orient readers, we recom-Metaxygnathus from Australia and Sinostega from China, mend that you repeatedly examine Figure 1.1 while are known from Gondwana. It is probable that additional reading the text. The first (but not the most primitive) tet-discoveries in northern Gondwana and

China will support rapod found was Ichthyostega (Ichthyo = fish; stega =

a global distribution of early tetrapods.

roof). For many years, this abundant fossil and another About 30–40 million years (a short time, geologically fossil, Acanthostega, represented by a few skull frag-speaking) after the first tetrapods appeared, two lineages, ments, were the only known tetrapods. In 1985, Tulerpe-amphibians and anthracosaurs, gave rise to all extant tetra-ton was discovered in Russia. The next discoveries of pods. Reptiles evolved from one descendent lineage of the tetrapods were made because of a fortuitous event. In early anthracosaurs. These evolutionary events occurred in 1971, a graduate student conducting a sedimentology landscapes that appeared alien compared to the familiar project in Greenland collected tetrapods that were placed landscapes of today. Plants, like animals, were only begin-in a museum but never studied. When these specimens ning to radiate into terrestrial environments from a were examined more closely, they were recognized as completely aquatic existence. Upland deserts consisted of Acanthostega. This discovery led to a resurgence of bare rock and soil. Plants grew only in valleys and along interest in early tetrapods, and many other fossils present the coasts where water was abundant. Early diversification in museums from previous work were reexamined and of terrestrial arthropods was underway, which clearly studied in detail. Additional material of various species affected amphibian and reptile diversification by providing made it easier to identify fragments that had not previ-a rich and abundant food supply.

ously been recognized as tetrapods. In addition, new We first examine what some of the key fossils tell us.

techniques such as CT (computed tomography) scanning We then summarize some of the morphological, and sen-allowed reinterpretations of previously collected mate-sory, respiratory, and feeding system changes that were rial. The result of the study of this material led to associated with the invasion of land.

Pipa (Pipidae)

Dendrosophus (Hylide) *Lithobates* (Ranidae) *Siren* (Sirenidae) *Ambystoma* (Ambystomatidae) *Siphonops* (Caecliidae) FIGURE 1.2 A sampling of adult body forms in living amphibians.

Although many details are uncertain, five to seven well-Elpistostege, Tiktaalik, Acanthostega, Ichthyostega, and known key fossils illustrate the transition from fish to tetra-Tulerpeton.

pod (Fig. 1.4). Tetrapods arose from osteolepiform lobe-Eusthenopteron—A tristichopterid fish, more or less con-finned fishes represented in this figure by Eusthenopteron.

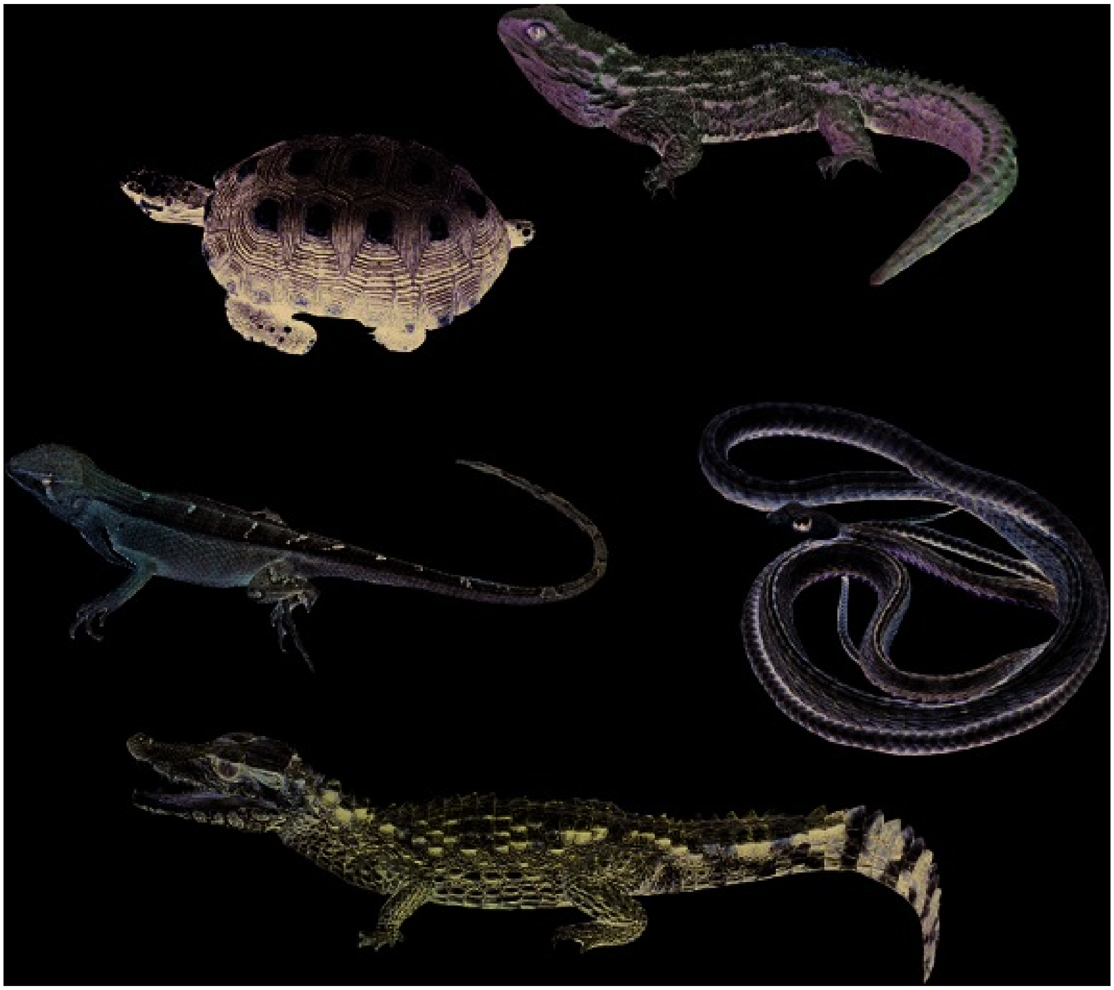
temporary with Acanthostega. Eusthenopteron is a Panderichthys and temporary with Acanthostega, Eusthenopteron is a Panderichthys and Tiktaalik were large, flat predatory fish member of the tetrapod stem group. It is convergent considered transitional forms between osteolepiform fishes with tetrapods in many respects, including having and tetrapods. They had strong limb-like pectoral fins that enlarged pectoral fins, and a flat, elongate snout enabled them to support their bodies and possibly move (Fig. 1.4). As a whole, fishes in this group (also out of water. Acanthostega and Ichthyostega were primitive including rhizodontids and osteolepidids) were ambush tetrapods. All of these species ranged in size from 0.75 to predators that lived in shallow waters.

1.5 m in length. Many other important fossils from this Panderichthys—This large Middle Devonian elpistoste-period exist (e.g., Fig. 1.1), each with its own place in the galian sarcopterygian fish from Latvia that lived 385

story of tetrapod evolution, and we refer the interested reader million years ago is the best-known transitional proto-to the paleontological literature for more details on these.

tetrapod. Complete specimens are available from the Middle to Late Devonian. It had a flat head, long Key Fossils

snout, and dorsally situated eyes (Fig. 1.4). The tetra-Because of their importance in reconstructing the evolu-pod-like humerus was dorsoventrally flattened, pre-tionary history of tetrapods, we comment briefly on seven sumably lending strength for support of the body, of the key fossil genera, Eusthenopteron, Panderichthys, although the fins have fin rays, not digits. A midline



Geochelone (Testudinidae) *Sphenodon* (Sphenodontidae) *Chironius* (Colubridae) *Stenocercus* (Tropiduridae) *Paleosuchus* (Alligatoridae) FIGURE 1.3 A sampling of adult body forms in living reptiles.

fin is present only on the tail. Panderichthys was a Primitive features included rhombic, overlapping predatory fish that may have used its fins to “walk” in scales like Panderichthys, lack of a dorsal fin, paired shallow freshwater swamps.

pectoral and pelvic fins with lepidotrichia (fin rays), Elpistostege—This elpistostegalian sarcopterygian fish and a generalized lower jaw. Derived features in Tik-from the early Late Devonian of Canada is most taalik included a flat body with raised, dorsal eyes, a closely related to Tiktaalik (Fig. 1.4). It is known only wide skull, and a mobile neck. The robust forefin and from skull and backbone fragments, but has long been pectoral girdle indicated that it was capable of sup-recognized as an intermediate form. Elpistostege, porting itself on the substrate. These features repre-unlike Tiktaalik, appears to have occurred in an estu-sent a radical departure from previously known, more arine habitat, possibly indicating that these fishes as a primitive sarcopterygian fishes. Discovery of an group were exploiting a variety of habitats.

intermediate fossil such as Tiktaalik helps to visualize Tiktaalik—The recent discovery of many specimens of the mosaic pattern of morphological changes that this elpistostegalian sarcopterygian from a single Late occurred during the transition from sarcopterygian Devonian locality in Arctic Canada greatly improved fishes to the earliest tetrapods. In fish, breathing and our understanding of the transition to tetrapods within feeding are coupled because taking water in over the fishes. This species may prove as significant as the gills in a sucking motion also pulls in food. These well-known Archaeopteryx, a fossil that represents the features became separated in Tiktaalik. The longer divergence of birds within reptiles. Phylogenetically, skull and mobile neck allowed a quick snap of the Tiktaalik, with Elpistostege, is apparently sister to head to capture prey.

Acanthostega + Ichthyostega. In many ways, Tiktaalik Acanthostega—This primitive transitional Late Devonian was like Panderichthys—both had small pelvic fins tetrapod from Greenland lived 365 million years ago.

with fin rays and well-developed gill arches, evidence Study of this best-known tetrapod changed our under-that both were aquatic (Fig. 1.4). Tiktaalik had a standing of early tetrapod evolution. The forelimb combination of primitive and derived features.

clearly had eight digits, but the limb had no wrist

Fossil

Body Form

Fin/Foot

Tulerpeton

Ichthyostega

Acanthostega

Tiktaalik

Panderichthys

Eusthenopteron

Glyptolepis

FIGURE 1.4 Relationships, body forms, and limb structure of the seven key fossil vertebrates used to recover the evolution of supportive limbs in tetrapods. Glyptolepis is the outgroup. Adapted from Ahlberg and Clack, 2006; Clack 2006; Daeschler et al., 2006; and Schubin et al., 2006.

bones or weight-bearing joints, thus showing that It had a forelimb with seven digits in a unique pattern.

limbs with digits evolved while these animals lived in Four main digits formed a paddle bound together by water and that they most likely did not have the ability stiff webbing, and three smaller digits formed a to walk (Fig. 1.4). Because the limb is similar to the leading edge (Fig. 1.4). Twenty-six presacral imbri-fish Eusthenopteron, it is considered to be primitive.

cate ribs were present. It had a true fish tail with fin Acanthostega had 30 presacral ribs; the fishlike ribs rays but may have had some ability to move about on were short and straight and did not enclose the body.

land. Based on overall skeletal morphology, It had a true fish tail with fin rays; the tail was long Ichthyostega likely had some ability for dorsoventral and deep, an indication that it was a powerful swim-flexion of the spine, and the limbs may have moved mer, and it had fishlike gills. Of 41 features unique together rather than alternately. Preparation of to tetrapods, Acanthostega had two-thirds of them.

recently collected material revealed that the auditory It had a large stapes that remains as part of the audi-apparatus is adapted for underwater hearing.

tory system of more recent tetrapods. The lower jaw Ichthyostega may have lived in freshwater streams of Acanthostega bore the inner tooth row on the coronoid and may have been able to move about on land to bone, a feature indicative of a tetrapod and not a fish. This some extent.

finding led to a close study of other jaw fragments already Tulerpeton—This primitive Devonian tetrapod from present in museums; these jaw fragments could now be Russia was described in 1984. Both the forelimb and distinguished as either fish or tetrapod. Acanthostega hindlimb had six digits (Fig. 1.4). The robust shoul-most likely lived in freshwater rivers.

der joint and slender digits indicate that Tulerpeton Ichthyostega—A primitive Late Devonian tetrapod from was less aquatic than either Acanthostega or Greenland, Ichthyostega lived 365 million years ago.

Ichthyostega.

Major Features of Early Tetrapod

Movement

Evolution

The transformation of fins to limbs was well underway The radiation of elpistostegalian fish (Panderichthys, Elpis-before early tetrapods moved to land. The cause remains tostege, and Tiktaalik) indicates that the tetrapod origin was debatable, but fleshy fins seem a prerequisite. The fleshy within the Euramerican landmass. Panderichthys and Elpis-fins of sarcopterygian fish project outward from the body tostege are found in deltaic and estuarine settings, but Tik-wall and contain internal skeletal and muscular elements taalik is found in nonmarine sediment, indicating that the that permit each to serve as a strut or prop. Because limbs elpistostegalian fishes were exploiting new habitats.

evolved for locomotion in water, presumably initially for Although changes occurred in nearly all systems during slow progression along the bottom, they did not support the transition from water to land, it remains difficult to heavy loads because buoyancy reduced body weight. The determine which changes preadapted tetrapod ancestors to fin-limbs probably acted like oars, rowing the body for-move to land (exaptation) and which represent true ward with the fin tips pushing against the bottom. Shifting responses (adaptations) to the transition.

from a rowing function to a bottom-walking function required bending of the fin-limb to allow the tip to make broader contact with the substrate (Fig. 1.6). The under-Respiration lying skeletal structure for this is evident in Tiktaalik Lungs appeared early in the evolution of bony fishes, long (Fig. 1.4). Bends or joints would be the sites of the future before any group of fishes had other terrestrial adapta-elbow–knee and wrist–ankle joints. As flexibility of the tions. Indeed, lungs are the structural predecessors of joints increased, limb segments developed increased mobil-swim bladders in the advanced fishes. Lungs may have ity and their skeletal and muscular components lost the sim-developed as accessory respiratory structures for gaseous ple architecture of the fin elements. Perhaps at this stage, exchange in anoxic or low-oxygen waters. The lung struc-fin rays were lost and replaced by short, robust digits, and ture of the fish–tetrapod ancestor and the earliest tetrapods the pectoral girdle lost its connection with the skull and is unknown because soft tissue does not readily fossilize.

allowed the head to be lifted while retaining a forward ori-Presumably lungs formed as ventral outpocketings of the entation as the limbs extended and retracted. The ichthyos-pharynx, probably with a short trachea leading to either tegalians represent this stage. Their limb movements, an elongated or a bilobed sac. The internal surface may although in water, must have matched the basic terrestrial have been only lightly vascularized because some cutane-walking pattern of extant salamanders, i.e., extension– ous respiration was also possible. Respiration (i.e., ventila-retraction and rotation of the proximal segment, rotation tion) depended upon water pressure. A fish generally rose of the middle segment (forearm and crus), and flexure of to the surface, gulped air, and dived (Fig. 1.5). With the the distal segment (feet). As tetrapods became increasingly head lower than the body, water pressure compressed the terrestrial, the vertebral column became a sturdier arch with buccal cavity and forced the air rearward into the lungs, stronger intervertebral links, muscular as well as skeletal.

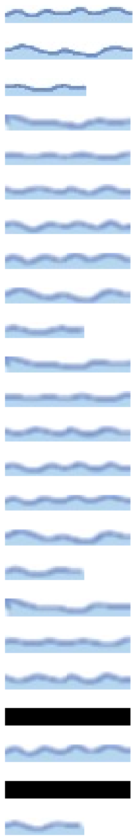
since water pressure was lower on the part of the body higher The limb girdles also became supportive—the pelvic gir-in the water column. Reverse airflow occurred as the fish dle by a direct connection to the vertebral column and surfaced headfirst. This mechanism is still used by most the pectoral girdle through a strong muscular sling air-breathing fish for exhalation. The fossil record provides connected to the skin and vertebral column. Although additional insight on this. Gills were present in the fish– stem tetrapods (e.g., Acanthostega) had more than five tetrapod ancestor but presumably absent in adult ichthyoste-digits, pentadactyly (five digits) predominates in descen-galians. The tetrapodomorph fish Tiktaalik occurred in shal-dent clades. The gallans. The tetrapodomorph fish Tiktaalik occurred in shal-dent clades. The evolution of pentadactyly and terrestrial-low, wandering streams in tropical or subtropical climates.

ity appear closely linked. The recently discovered This type of habitat selected for respiratory advances such Pederpes finneyae, a terrestrial tetrapod from the end of as the buccal and costal pumping mechanisms employed the Early Carboniferous, probably has the earliest hind-by tetrapods. The broad skull allows space for the buccal limb capable of walking.

pumping. An enlarged spiracular tract led to respiratory modifications that allowed breathing in aquatic–terrestrial Feeding

habitats. The buccal-force pump replaced a passive pump mechanism. Air entered through the mouth with the floor The presence of a functional neck in Tiktaalik provides depressed, the mouth closed, the floor contracted (elevated) some insight into the early evolution of inertial feeding, and drove air into the lungs, and the glottis closed, holding in which the mouth–head of the tetrapod must move for-the pulmonary air at supra-atmospheric pressure. Exhalation ward over the food. While in the water, the fluidity and resulted from the elastic recoil of the body wall, driving air resistance of water assisted in grasping and swallowing outward. Thus respiratory precursors for invasion of land food. In shallow water or out of water, the ability to were present in aquatic tetrapod ancestors.

move the head would provide a substantial advantage



air flow

air

air flow

opercula

mouth

buccal floor

close

closed

depressed

air held in

buccal cavity

lungs

air exits via

air exits via

mouth and

buccal floor

operculum

pumps air

to lungs

lungs

air into

buccal cavity

FIGURE 1.5 Air-breathing cycle of the longnosed gar (Lepisosteus osseus). As the gar approaches the surface at an angle, it drops its buccal floor and opens its glottis so air can escape from the lungs (bottom center, clockwise). By depressing the buccal floor, the gar flushes additional air from the opercular chamber. Once flushed, the gar extends its snout further out of the water, opens its mouth, depresses the buccal floor drawing air into the buccal cavity, and shuts the opercula. The mouth remains open and the floor is depressed further; then closing its mouth, the gar sinks below the surface. Air is pumped into the lungs by elevating the buccal floor. Adapted from Smatresk, 1994.

Skin

in capturing prey. Several modifications of the skull may have been associated with this feeding behavior. With The skin of larval amphibians and fish is similar. The epi-the independence of the pectoral girdle and skull, the dermis is two to three layers thick and protected by a skull could move left and right, and up and down on mucous coat secreted by numerous unicellular mucous the occipital condyles–atlas articulation. The snout and cells (Chapter 2). The skin of adult amphibians differs from jaws elongated. The intracranial joint locked and the pri-that of fish ancestors. The epidermis increased in thickness mary palate became a broader and solid bony plate.

to five to seven layers; the basal two layers are composed of

Actinopterygii

organs function only in water and occur only in the aquatic phase of the life cycle or in aquatic species. Hearing and middle ear structures appeared. The early tetrapod Ichthyostega has a unique specialized ear, and the middle ear was modified in early tetrapods. Changes in eye structure evolved in early tetrapods sharpening their focus for aerial vision. The nasal passages became a dual channel, with air passages for respiration and areas on the surfaces modified for olfaction.

Osteolepiformes

The preceding summarizes the major anatomical altera-tions that occurred in the transition to tetrapods within fishes. Many physiological modifications also occurred; some of these are described in Chapter 6. Some aspects, like reproduction, remained fishlike: external fertilization, eggs encased in gelatinous capsules, and larvae with gills.

Actinistia

Metamorphosis from the aquatic larval to a semiaquatic adult stage was a new developmental feature. The unique morphological innovations in the stem tetrapods illustrate the divergent morphology and presumably diverse ecology of these species. This diversification was a major feature of the transition from water to land.

Porolepiformes

EVOLUTION OF EARLY ANAMNIOTES

Ancient Amphibians

Dipnoi

Given the existing fossil record, clearly defining Amphibia is a challenge. The monophyly of living amphibians, the Lissamphibia (caecilians, frogs, and salamanders) seems highly probable, and they are members of the temnospondyl clade. The assignment of extinct taxa to the Temnospondyli is more controversial. Edops (Fig. 1.7) and Tetrapoda

relatives, Eryops and relatives, trimerorhachoids, and a diverse assortment of taxa labeled dissorophoids make up the major groups of extinct temnospondyls. Aistopods, baphetids (= Loxommatidae), microsaurs, and nectrides FIGURE 1.6 Fin and limb skeletons of some representative fishes and *Edops*

Paleothyris

tetrapods. Top to bottom, rayfinned or actinopterygian fin, osteolepiform premaxillary lobed fin, actinistian lobed fin, porolepiform lobed fin, lungfish or dip-noan lobed fin, and a tetrapod limb. Adapted from Schultze, 1991.

nasal

lacrimal

maxillary

living cells and are equivalent to fish or larval epidermis.

frontal

The external layers undergo keratinization and the mucoid prefrontal

cuticle persists between the basal and keratinized layers.

postfrontal

Increased keratinization may have appeared as a protection parietal

jugal

against abrasion, because terrestrial habitats and the low postorbital

body posture of the early tetrapods exposed the body to supratemporal

constant contact with the substrate and the probability of squamosal

greater and frequent surface damage.

quadrato—

tabular

jugal

quadrate

inter—

postparietal

tabular

postparietal

temporal

Sense Organs

FIGURE 1.7 Comparison of the skulls of an early amphibian Edops As tetrapods became more terrestrial, sense organs shifted and an early reptile Paleothyris. Scale: bar = 1 cm. Reproduced, with per-from aquatic to aerial perception. Lateral line and electric mission, from Museum of Comparative Zoology, Harvard University.

have been identified as amphibians, although their relation-lacuna in the squamosal bone that may have housed a tym-ships remain controversial. The baphetids are not amphi-panum. Neither salamanders nor caecilians have tympana, bians; presumably they are an early offshoot of the early although they have greatly reduced middle ears, suggest-protoamniotes and possibly the sister group of the anthraco-ing the loss of the outer ear structures.

saurs. Details on the appearance and presumed lifestyles A number of other unique traits argue strongly for the of these extinct groups are provided in Chapter 3. All monophyly of the Lissamphibia. All share a reliance on cuta-these groups may have had their origins in the Early neous respiration, a pair of sensory papillae in the inner ear, Carboniferous, and only a few lineages survived and pros-two sound transmission channels in the inner ear, specialized pered into the Permian. As an aside, the lepospondyls visual cells in the retina, pedicellate teeth, the presence of and labyrinthodonts were once widely recognized groups two types of skin glands, and several other unique traits.

of extinct amphibians. The members of the lepospondyls Three structures, gills, lungs, and skin, serve as respi-

(= Aistopoda + Microsauria + Nectridea) shared features ratory surfaces in lissamphibians; two of them frequently associated with small body size and aquatic behavior, function simultaneously. Aquatic amphibians, particularly but not features of phylogenetic relatedness that would larvae, use gills; terrestrial forms use lungs. In both air and support the monophyly of lepospondyls (Fig. 1.1). The water, the skin plays a major role in transfer of oxygen labyrinthodonts encompassed phylogenetically unrelated and carbon dioxide. One group of terrestrial amphibians, taxa united by shared primitive (ancestral) characters.

the plethodontid salamanders, has lost lungs, and some Thus, the groups were polyphyletic and their use has been aquatic taxa also have lost lungs or have greatly reduced largely discontinued.

ones; these amphibians rely entirely on cutaneous respira-By defining Amphibia by its members, it is possible tion. All lunged species use a force-pump mechanism for to identify unique characters shared by this group. These moving air in and out of the lungs. Two types of skin characters are surprisingly few: (1) the articular surface of glands are present in all living amphibians: mucous and the atlas (cervical vertebra) is convex; (2) the exoccipital granular (poison) glands. The mucous glands continuously bones have a suture articulation to the dermal roofing secrete mucopolysaccharides, which keep the skin surface bones; and (3) the hand (manus) has four digits and the foot moist for cutaneous respiration. Although the structure of (pes) five digits. Other features commonly used to charac-the poison glands is identical in all amphibians, the toxic-terize amphibians apply specifically to the lissamphibians, ity of the diverse secretions produced is highly variable, although some of them may apply to all Amphibia but are ranging from barely irritating to lethal to predators.

untestable because they are soft anatomical structures that The auditory system of amphibians has one channel have left no fossil record.

that is common to all tetrapods, the stapes–basilar papilla channel. The other channel, the opercular–amphibian papilla, allows the reception of low-frequency sounds (< 1000 Hz).

Modern Amphibians—The

The possession of two types of receptors may not seem Lissamphibia

peculiar for frogs because they are vocal animals. For the largely mute salamanders, a dual hearing system seems The living amphibians are generally thought to share peculiar and redundant. Salamanders and frogs have a common ancestor and, hence, to represent a monophy-green rods in the retina; these structures are presumably letic group. Numerous patterns of relationship have been absent in the degenerate-eyed caecilians. Green rods are proposed, but only three patterns continue to have time-found only in amphibians, and their particular function tested evidence and advocates. The proposed patterns are remains unknown.

(1) frogs arose from a different ancestor than salamanders The teeth of modern amphibians are two-part struc-and caecilians; (2) frogs and salamanders

are a sister tures: an elongate base (pedicel) is anchored in the jaw-group, and caecilians are a sister group to their clade; bone and a crown protrudes above the gum. Each tooth (3) caecilians and salamanders are a sister group, and is usually constricted where the crown attaches to the ped-frogs are a sister group to their clade. The preponderance icel. As the crowns wear down, they break free at the con-of evidence argues for monophyly and probably a dissoro-striction and are replaced by a new crown emerging from phid ancestry. Remaining uncertainty derives from the within the pedicel. Only a few living amphibians lack ped-long time gap between the potential temnospondyl ances-icellate teeth. Among extinct amphibians, pedicellate teeth tors in the Upper Carboniferous and the occurrence of occur in only a few dissorophids.

all three groups in the Early to Middle Jurassic. These Living amphibians possess other unique traits. All have Jurassic forms show the major characteristics of their fat bodies that develop from the germinal ridge of the extant descendants but few traits of ancient amphibians.

embryo and retain an association with the gonads in adults.

Only the Lower Triassic frog, Triadobatrachus massinoti, Frogs and salamanders are the only vertebrates able to raise from Madagascar, shows a possible link to the dissorophid and lower their eyes. The bony orbit of all amphibians temnospondyls. T. massinoti shares with them a large opens into the roof of the mouth. A special muscle stretched

across this opening elevates the eye. The ribs of amphibians The evolution of terrestrial forms required modifications in do not encircle the body.

anatomy, physiology, behavior, and a host of other character-This large number of unique similarities argues strongly istics. True terrestriality required major reorganizations of life-for the shared ancestry of the living amphibian groups.

style and life processes. The shifts from eggs that required Whether salamanders and frogs or salamanders and caeci-water or moisture for deposition to those that could withstand lians are sister groups remains unresolved; different data dry conditions and from free-living embryos to direct develop-sets and analyses support one or the other of these pairs, ment was critical in the move to land, but other adaptations but not a frog–caecilian sister relationship.

were also required. Movement and support without the support of water required adjustments in the musculoskeletal system.

EVOLUTION OF EARLY AMNIOTES

Feeding in air required behavioral and morphological shifts, as did the use of different prey and plant materials for food.

Early Tetrapods and Terrestriality

Gravity, friction, abrasion, and evaporation obligated modification of the integument for protection and support and Fully terrestrial tetrapods presumably arose in the Early internal mechanisms to regulate water gain and loss. Modifica-to Middle Mississippian period (360–340 mybp; Lower tion was not confined to the preceding anatomical and physio-Carboniferous). Uncertainty arises because few tetrapod logical systems. These changes did not occur synchronously; fossils are known from this period. Tetrapod fossils appear some were linked, others were not; some required little modi-with high diversity in the Late Mississippian and Early fication because of exaptation (“preadaptation”), and others Pennsylvanian (340–320 mybp). The diversity includes required major reorganization. The diversity of changes is the first radiation of the amphibians and the appearance reflected in the diversity of Lower Carboniferous amphibians of the anthracosaurs and the earliest amniotes. This inter-and the polyphyletic anthracosaurs.

val saw the emergence of waterside from shallow-water Amphibians remained associated with aquatic habitats, forms and to increasingly abundant and diverse terrestrial and several independent clades moved at least partially forms. Unlike the largely barren landscape of the Late to land. Many of these were successful in terms of high Devonian during the transition from fish to tetrapod, Car-abundance or diversity and geologic longevity. Neverthe-boniferous forests were widespread, composed of trees less, amphibians remained tied to moisture. As amphibians 10 m, and taller, probably with dense understories. Plant diversified in association with aquatic habitats, an increasing communities were beginning to move into upland areas.

number of anthracosaurs and their descendants shifted to While plants diversified on land, invertebrates and verte-terrestriality in all phases of their life (Fig. 1.8; Table 1.3).

brates were also evolving terrestrial residents.

These are represented today by the amniotes (Amniota).

FIGURE 1.8 A branching diagram of the evolution within the Tetrapoda, based on sister group relationships. The diagram has no time axis, and each name represents a formal clade-group name. After Clack, 1998; Gauthier et al., 1988a,b, 1989; and Lombard and Sumida, 1992; a strikingly different pattern is sug-Ichthyostegalia Nectridea

Aistopoda

Microsauria

Gymnophiona

Anura

Caudata

Baphetidae

Anthracosauroidea

Seymouriamorpha

Diadectomorpha

Synapsida

Mesosauria

Parareptilia

Eureptilia

gested by Laurin and Reisz, 1997.

Temnospondyli

Reptilia

Amniota

Cotylosauria

Amphibia

Batrachosauria

Anthracosauria

Tetrapoda

drove the replacement of gelatinous capsules by the depo-TABLE 1.3 A Hierarchical Classification sition of an increasingly thicker calcareous shell and the of Anthracosaur Descendents.

shift of egg deposition to drier sites. Recent modification of this hypothesis has placed more emphasis on the devel-Tetrapoda opment of the fibrous envelope precursor to the shell and Amphibia

Anthracosauria

the supportive role of such an envelope for a large-yolked Anthracosauroidea

egg. Other scenarios, such as the “private pool” theory, Batrachosauria

have directed attention to the development of the extraem-Seymouriamorpha bryonic membranes and their encapsulation of the egg or Cotylosauria

embryo. Each hypothesis has a facet that reflects an aspect Diadectomorpha

of the actual evolutionary history, but none provides a Amniota

full explanation. Lacking historical data (fossils), we can-Synapsida not determine whether the amniotic membranes evolved Reptilia

in embryos held within the female’s oviduct or whether Note: This classification derives from the sister-group relationships displayed in they evolved in externally shed eggs. Either explanation Figure 1.7. Because of the hierarchial arrangement, a reptile or mammal is an is equally parsimonious from available information on anthracosaur, although paleontologists commonly use anthracosaur to refer to the extinct tetrapod groups that are not Amphibia but also likely not Amniota.

extant vertebrates (Fig. 1.9). Similarly, we cannot determine when and how a fibrous envelope replaced the sarcopterygian’s gelatinous envelope, although a fibrous “shell”

likely preceded a calcareous one because calcium crystals Full terrestriality required that organisms have the abil-are deposited in a fibrous matrix in all living reptiles.

ity to reproduce and develop without freestanding water.

Juveniles and adults also required a protective enve-The evolution of the amniotic egg, which could be depos-lope because of the desiccative effect of terrestrial life.

ited on land and could resist dehydration, solved this problem (see Chapter 2 for anatomical details; note that many reptilian eggs still must absorb moisture to complete development). Internal fertilization set the stage for production of closed (shelled) eggs. By enclosing an embryo in a sealed chamber (shelled egg), the evolution of extraembryonic membranes not only provided embryos with protection from the physical environment, but also provided a Seymouriamorpha

Diadectomorpha

Synapsida

Mesosauria

Testudines

procolophonoids

Pareiasauria

Millerettidae

Captorhinidae

Paleothyris

Araeoscelidia

Sauria

reservoir for metabolic waste products.

Internal fertilization is not a prerequisite for direct development, nor does direct development free the parents Diapsida

from seeking an aquatic or permanently moist site for egg deposition. Among extant amphibians, internal fertilization predominates in caecilians and salamanders, but only Parareptilia

Eureptilia

a few anurans with direct development have internal fertilization. When an egg is encased in a protective envelope, the encasing process must be done inside the female’s reproductive tract, and if sperm is to reach the egg–ovum Reptilia

surface, the sperm must be placed within the female’s Amniota

reproductive tract as well. Sperm delivery and fertilization must precede egg encasement.

Because internal fertilization has arisen independently in the three extant amphibian clades, it is reasonable to Anthracosauria

assume that internal fertilization could easily arise in pro-FIGURE 1.9 A branching diagram of the evolution of basal Amniota and toamniote anthracosaurs. One problem with the fossil early reptiles, based on sister group relationships. The diagram has no time record for early tetrapods is that anamniotic eggs do not axis, and each capitalized name represents a formal clade-group name.

readily fossilize (there are no hard parts), and as a conse-Opinion varies on whether the mesosaurs are members of the Reptilia clade quence it is difficult to reconstruct events leading to the or the sister group of Reptilia. If the latter hypothesis is accepted, the Mesosauria and Reptilia comprise the Sauropsida. Turtles (Testudines) are shown evolution of internal fertilization and the shift to shelled here as nested within the Parareptilia based on morphology. More recent eggs. The common scenario suggests that naked amniotic molecular analyses indicate that they are nested in the Eureptilia (see Chap-eggs with direct development were laid first in moist ter 18). After Gauthier et al., 1989; Laurin and Reisz, 1995; and Lee, 1997; areas. Selection to reduce predation by microorganisms a strikingly different pattern is suggested by deBraga and Rieppel, 1997.

Changes in skin structure are invisible in the fossil record, articulation with the glenoid fossa. The shoulder or pecto-but the skin of present-day amphibians suggests that the ral girdle lost dermal bone elements but remained large.

initial evolutionary steps were an increase in skin thick-The iliosacral articulation was variable and depended ness by adding more cell layers and keratinization of the upon the size and robustness of the species, although two keratinization of the upon the size and robustness of the species, although two external-most layer(s). Keratinization of skin effectively sacral ribs usually attached to each ilium. Hindlimbs com-reduces frictional damage and the penetration of foreign monly were larger and sturdier, demonstrating their objects but appears to be ineffectual in reducing water increasing role in propulsion.

loss. Early modifications of the integument were also The skull became more compact and tightly linked, driven by its increased role in the support of internal although it was still massive in many anthracosaurs and early organs to compensate for the loss of buoyancy and com-amniotes (Fig. 1.7). A major trend was the reduction of the pression of water. These changes occurred in deep dermal otic capsule in early tetrapods, without the concurrent devel-layers and involved altering fiber direction and layering.

opment of structural struts; thus, the skull roof and braincase Associated with increasingly impermeable skin (effec-became weakly linked. Different strengthening mechanisms tively reducing cutaneous respiration) was the shift to more appeared in different lineages. The diadectomorphs and rep-effective pulmonary respiration. The first modifications of tiles shared the unique development of a large supraoccipital lungs were probably an increase in size and internal parti-bone to link the braincase and skull roof. The cheek to brain-tioning. The latter is commonly associated with increased case solidification occurred in three general patterns within vascularization. Once again, these modifications apparently the amniotes. The anapsids developed a strong attachment occurred in the protoamniotes. When and where they of the parietal (skull roof) to the squamosal (cheek) along occurred can be partially identified by examining rib struc-with a broad and rigid supraoccipital attachment. In the di-ture and the appearance of a complete rib cage. A rib cage apsids, the opisthotic extended laterally to link the braincase (thoracic basket) signals the use of a thoracic respiratory to the cheek. A lateral expansion of the opisthotic also pump for ventilation of the lungs. The rib cage appears occurred in the synapsids but in a different manner.

incomplete in most anthracosaurs and seymouriamorphs, The robust stapes with its broad foot plate was a criti-so those groups probably were still largely dependent on cal strut in the strengthening of the skull. This role as a the buccal force pump. The rib cage of diadectomorphs supportive strut precluded its function as an impedance extends further ventrally; although it still appears incom-matching system (see the discussion of ears in Chapter 2).

plete, this condition may mark the transition from buccal Later, the opisthotic became the supportive unit, and the to thoracic ventilation.

stapes (columella) became smaller and took on its auditory Anthracosaurs and early amniotes lacked otic notches, role. This change occurred independently in several reptil-denoting the absence of eardrums. Although not deaf, they ian lineages; although the results are the same, the evolu-were certainly insensitive to high-frequency sounds. It is tionary route to the middle ear of turtles differed from doubtful that their olfactory sense was as limited. Well-that of the archosaurs and lepidosaurs. The synapsids fol-developed nasal passages in fossils and the presence of lowed an entirely different route and evolved the unique highly developed olfactory organs in living reptiles indicate three-element middle ear seen today in mammals.

that this sense was well developed in the earliest amniotes.

Nasal passages contained conchae, which may have aided Early Amniotes

in the reduction of water loss. Eyes were also likely well developed at this stage, for vision is extremely important The Amniota derives its name from the amniotic egg, in foraging and avoiding predators in an aerial environment.

a synapomorphy shared by all members (Fig. 1.9 and Locomotory and postural changes for a terrestrial life Fig. 1.10). Other anthracosaurs may have had amniotic are reflected in numerous changes in the postcranial skel-eggs, although they are not classified as amniotes. A fossil eton. Vertebral structure changed to produce a more robust taxon cannot be identified as an amniote or anamniote by supporting arch. The pleurocentrum became the main structure of its egg, because few fossil eggs of anthraco-component of the vertebral body, displacing the intercen-saurs have been found. Further, no eggs have been found trum forward and upward. Neural arches became broader, in association with an adult’s skeleton or with a fossil zygapophyses tilted, and regionalization of neural spine embryo showing extraembryonic membranes. Bony traits height occurred, yielding differential regional flexibility must be used to determine which taxa are amniotes and with an overall strengthening of the vertebral column.

which ones are not, and there is no unanimity in which Modification of the two anterior-most cervical vertebrae bony traits define an amniote. Indeed, amniotes are com-

(atlas–axis complex) stabilized lateral head movement monly defined by content; for example, Amniota comprise during walking and running. Modifications in the limb the most recent common ancestor of mammals and reptiles and girdle skeletons are not as evident in the early anthra-and all of its descendants.

cosaurs as those appearing in later amniotes. The humerus Unquestionably, anthracosaurs are the ancestral stock remained a robust polyhedral element that had a screwlike that gave rise to the amniotes (Fig. 1.1 and Fig. 1.9). They

Extended embryo retention

features do not suggest that they were deaf, but that their unordered

hearing was restricted to low frequencies, probably less *Latimeria*

than 1000 Hz, much like modern-day snakes and other reptiles without eardrums. Possibly their development Dipnoi

included preamniotic changes, such as partitioning of the fertilized egg into embryonic and extraembryonic regions, Anura

or even a full amniotic state.

The first amniote fossils are from the Middle Pennsyl-Caudata vanian, but they are not primitive amniotes in the sense of displaying numerous transitional traits. These first amniotes Gymnophiona

are Archaeothyris (a synapsid), Hylonomus (a reptile), and Paleothyris (a reptile; Fig. 1.9); already the divergence Synapsida

of the synapsids and reptilian stocks was evident. The Synapsida is the clade represented today by mammals; they Testudines

are commonly called the mammal-like reptiles, an inappropriate and misleading name. The pelycosaurs were the first present

Crocodylia

major radiation of synapsids and perhaps gave rise to the Amniota

ancestor of the Therapsida, the lineage leading to modern absent

Aves

mammals

mammals.

polymorphic

Divergence among the basal reptiles apparently equivocal

Squamata

occurred soon after the origin of the synapsids, and again because of the absence of early forms and the later appear-FIGURE 1.10 Presence of the amnion defines the Amniota. Viviparity ance of highly derived reptilian clades, there is uncertainty is not necessarily associated with presence of an amnion. This distribution of egg-retention based on extant species does not permit the identifi-and controversy about the early evolutionary history of the cation of the condition in basal amniotes. The origin of terrestrial reptiles. The Mesosauria of the Lower Permian are consid-amniotic eggs as an intermediate stage is equally parsimonious with the ered a sister group to all other reptiles or a sister group to all evolution of amniotic eggs within the oviduct to facilitate extended egg other parareptiles (Fig. 1.9). Mesosaurs were specialized retention. After Laurin and Reisz, 1997.

marine predators, and their specializations have provided few clues to their relationships to other early reptiles.

possess features present in amniotes but not in Paleozoic Controversy surrounds the origin of turtles and or later amphibians. Anthracosaurs and amniotes share whether the Parareptilia is paraphyletic or monophyletic.

such features as a multipartite atlas–axis complex in which Recent discoveries and better preparation of old and new the pleurocentral element provides the major support.

fossils have led to a redefinition of the Parareptilia and Both possess five-toed forefeet with a phalangeal formula to its recognition as a clade including the millerettids, par-of 2,3,4,5,3 and a single, large pleurocentrum for each ver-eiasaurs, procolophonoids, and turtles. The latter two taxa tebra. These traits are also present in the seymouriamorphs are considered to be sister groups. However, another inter-and diadectomorphs.

pretation recognizes pareiasaurs and turtles as sister The seymouriamorphs are an early divergent group of groups. A strikingly different interpretation considers the anthracosaurs, although their fossil history does not begin turtles as diapsids and further suggests a moderately close until the Late Pennsylvanian.

These small tetrapods, some-relationship to lepidosaurs. Molecular data support the times incorrectly called amphibians, probably had external diapsid relationship by yielding a turtle–archosaur (croco-development and required water for reproduction. Signifi-dylian + bird) sister-group relationship or a turtle– cantly, neither the seymouriamorphs nor the diadecto-crocodylian one. These data support the idea that turtles morphs are amniotes (Fig. 1.9).

are more closely related to other living reptiles than to liv-The diadectomorphs shared a number of specialized ing mammals, but they do not provide information on the (derived) features with early amniotes—traits that are not early history of reptile evolution. As noted earlier in the present in their predecessors. For example, both groups discussion of fish–tetrapod relationships, molecular data lost temporal notches from their skulls, have a fully differ-yield a simple phylogeny of living taxa only. Relation-entiated atlas–axis complex with fusion of the two centra ships of extinct taxa and their sequence of divergence in adults, and possess a pair of sacral vertebrae. They based strictly on morphology add complexity to phylo-share a large, platelike supraoccipital bone and a number genies and often reveal relationships different from of small cranial bones (supratemporal, tabulars, and post-molecular-based phylogenies. One difficulty with molecu-parietals) that are lost in advanced reptiles. The stapes of lar studies is that, for early divergences, few taxa are used.

both were stout bones with large foot plates, and apparAs new taxa are added to the analyses, proposed relation-ently eardrums (tympana) were absent. These latter ships can change greatly. Nevertheless, it appears that the

best current data suggest that turtles are nested within diapsids, which we adopt here.

TABLE 1.4 A Hierarchical Classification of the Early Prior to the preceding studies, turtles were considered a Reptilia.

sister group to the captorhinids, and these two taxa were Amniota

the main members of the Anapsida, the presumed sister Synapsida

group of the Diapsida. The parareptiles were considered Reptilia

to be paraphyletic. In spite of the different placement of Parareptilia turtles, the preceding studies agree on the monophyly Millerettidae

of the parareptiles and the sister-group relationship of cap-unnamed torhinids to all other eureptiles (Fig. 1.9). Paleothyris Pareiasauria

unnamed

(Fig. 1.9) is one of the oldest eureptiles, although already procolophonoids

structurally derived from, and the potential sister group to, Eureptilia

all diapsid reptiles.

Captorhinidae

unnamed

Paleothyris

RADIATION OF DIAPSIDS

Diapsida

Araeoscelidia

Diapsida is a diverse clade of reptiles. It has a long taxonomic Sauria

Archosauromorpha

history and its member content is generally accepted with Archosauria

only minor controversy, excluding the current disagreement Pseudosuchia

about inclusion of turtles. Modern diapsids include lizards, Testudines

snakes, turtles, birds, and crocodylians; extinct diapsids Crocodylia

include dinosaurs, pterosaurs, ichthyosaurs, and many Ornithodira

other familiar extinct taxa. The stem-based name Diapsida Aves

is derived from the presence of a pair of fenestrae in the Lepidosauromorpha

temporal region of the skull; diapsids are also diagnosed Lepidosauria

Sphendontida

by a suborbital fenestra, an occipital condyle lacking an Squamata

exocciptal component, and a ridged-grooved tibioastraga-lar joint.

Note: This classification derives from the sister-group relationships in

Figures 1.8 and The earliest known divergence yielded the araeosceli-1.10.

dians, a short-lived group, and the saurians (Fig. 1.11, Table 1.4). The araeoscelidians were small (about 40 cm total length) diapsids of the Late Carboniferous and were an evolutionary dead end. In contrast, the saurian lineage gave rise to all subsequent diapsid reptiles. Members of the Sauria share over a dozen unique osteological features, including a reduced lacrimal with nasal–maxillary contact, no caniniform maxillary teeth, an interclavicle with dis-Araeoscelidia Lepidosauromorpha

Archosauromorpha

Ichthyosauria

Placodontia

plesiosaurs

tinct lateral processes, and a short, stout fifth metatarsal.

The Euryapsida apparently arose from an early split in the Sauria clade (Fig. 1.11). They comprise a diverse Sauropterygia

group of mainly aquatic (marine) reptiles, ranging from the fishlike ichthyosaurs to the walruslike placodonts and Euryapsida

the “sea-serpent” plesiosaurs. Individually these taxa and collectively the Euryapsida have had a long history of Sauria

uncertainty in their position within the phylogeny of reptiles. Only since the late 1980s has their diapsid affinity Diapsida

gained a consensus among zoologists, although different FIGURE 1.11 A branching diagram of the evolution of basal reptile interpretations about basal relationships remain. For exam-clades, based on sister-group relationships. The diagram has no time axis, ple, are they a sister group of the lepidosauromorphs or a and each capitalized name represents a formal clade-group name. Plesiosaurs is used as a vernacular name and is equivalent to Storrs’s (1993) sister group of the lepidosauromorph–archosauromorph Nothosauriformes. After Caldwell, M., 1996; Gauthier et al., 1989.

clade? Is the Ichthyosauria a basal divergence of the

Hypermorphic (hypermorphosis)

Pre-displaced (pre-displacement)

No change in trait offset

Must involve more than one pure

Isomorphic (isomorphosis)

Isotypic (isogenesis)

shape

perturbation

Source: Reilly et al., 1997.

set of traits can change in descendants without affecting the condition of that trait in the ancestral species or indivi-developmental timing and rates of other traits; paedogenesis duals, respectively. The male Plestiodon [Eumeces] lati-

(Table 2.2) is a common heterochronic event in amphi-ceps develops a very large head relative to head size in bians. These processes and the resulting patterns occur at its sister species P. fasciatus, which presumably represents two different scales, intraspecific and interspecific. Changes the ancestral condition. The larger head is an example of in a trait within populations (intraspecific) or a species peramorphosis; however, individuals within populations result in different morphs within the same population, such of P. laticeps have variable head size. This intraspecific as carnivorous morphs of spadefoot tadpoles. Differences in variation likely arises from sexual selection and represents a trait's development among species (interspecific) reflect peragenesis, assuming that a smaller head size is the popu-phylogenesis. These two levels of heterochrony and the lation's ancestral condition, a reasonable assumption con-complex interplay of heterochronic processes have led to sidering that females and juveniles have relatively small confusion and an inconsistent use of terms. Dr. Steve Reilly heads.

and his colleagues constructed a model that demonstrates Isomorphosis and isogenesis refer to a developmental some of this complexity and applies a set of terms making process in which a trait is identical to the trait in the ances-the process of heterochrony relatively easy to understand tral species or individuals, respectively, but the develop-

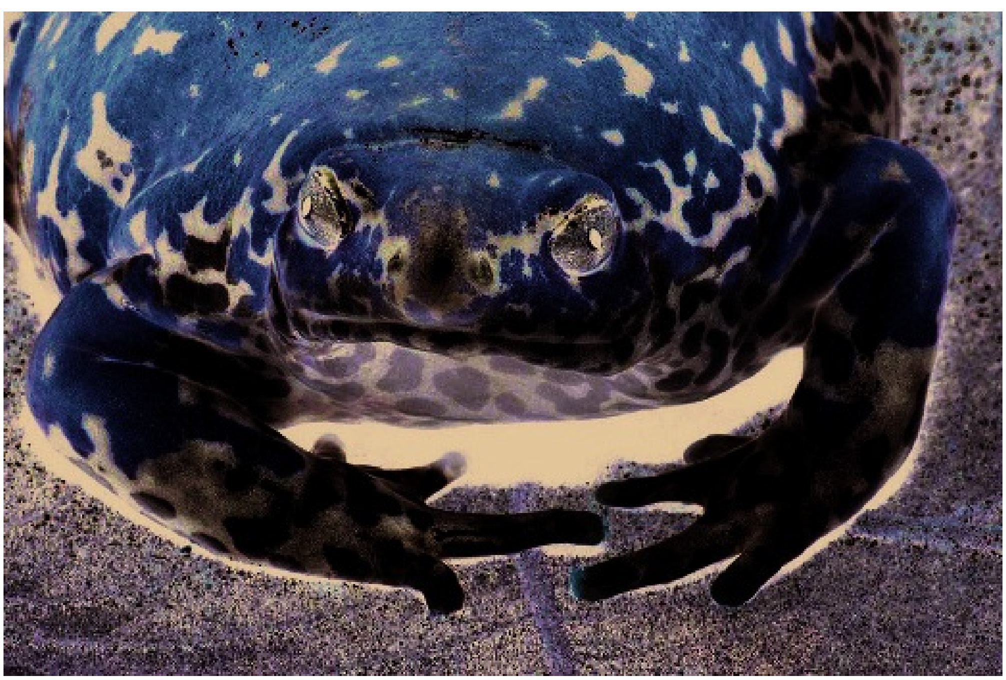
(Table 2.2). By understanding this simple model, much mental pathway is different. For isomorphy or isogenesis developmental variation within and among species can be to occur, development must undergo two or more hetero-attributed to heterochrony.

chronic processes in order to "counteract" differences in This simple model centers on developmental patterns developmental timing and speed. The various species of in an ambystomatid salamander in which individuals with the salamander Desmognathus display direct and indirect larval morphology as well as individuals with adult mor-development with variable durations of embryogenesis, phology can reproduce. Paedomorphosis and paedogene-yet embryogenesis, phology can reproduce. Paedomorphosis and paedogenic yet adult morphology (head shape, skull, and hypobran-sis refer to a developmental process in which a trait fails chial architecture) is nearly identical, exemplifying iso-to develop to the point observed in the ancestral species morphosis. Isogenesis occurs in Ambystoma talpoideum or individuals, respectively. The axolotl (Ambystoma mex-where adult terrestrial morphology is identical in those icanum) is a paedomorphic species. Morphological devel-individuals that underwent a typical developmental pattern opment of certain traits in the axolotl is truncated relative and in those individuals that were paedogenic (Fig. 2.2).

to that in its ancestral species Ambystoma tigrinum. Intras-pecifically, morphs of Ambystoma talpoideum with larval traits can reproduce, hence their morphological develop-EMBRYONIC LIFESTYLES

ment is truncated relative to their reproductive develop-Protective Barriers ment and thus they exhibit paedogenesis (Fig. 2.2). Many other examples exist. For example, the tiny head relative Tetrapod zygotes have barriers to protect them from predato body size in New World microhylids frogs likely repre-tion by micro-and macroorganisms, from physiological sents truncatation of head development (Fig. 2.3).

challenges, and from abiotic physical threats. For those Peramorphosis and peragenesis refer to a developmen-amphibians and reptiles with internal development, whether tal process in which a trait develops beyond the state or intra-or extrauterine, the parent’s body provides the shield;



Paedogenesis and isogenesis in *Ambystoma talpoideum* Normal species and

Delayed metamorphosis trajectory

ancestral trajectory

of some individuals

Isotypic

individuals

phosis

ity

xual

Se

matur

Metamor

Head “shape” axis

Paedotypic

individuals

Temporary delay in the

onset of metamorphosis

0

0.5

1.0

>1.0

Age (years)

FIGURE 2.2 Paedogenesis and isogenesis in Ambystoma talpoideum. The life history of A. talpoideum demonstrates the complexities of trait development patterns. The ancestral condition for this species is metamorphosis into a terrestrial salamander in less than one year. Under certain environmental conditions, paedogenesis occurs when metamorphosis is delayed and results in sexual maturation of the individual with retention of larval traits (i.e., the larval morphology) producing paedotypic individuals. Isogenesis occurs when similar early larvae follow different developmental trajectories but ultimately produce similar adults. The adults are termed isotypic individuals. Figure courtesy of S. M. Reilly.

however, for externally deposited zygotes (eggs), a protec-can be penetrated by a sperm in the cloaca or immediately tive barrier must be deposited around the ova before they upon release of eggs into the external environment. These are released to the outside. Amphibians encase their ova in layers form the gelatinous capsules and egg masses of several mucoprotein and mucopolysaccharide layers that amphibians (Fig. 4.4). Reptiles, which have internal fertiliza-tion, can encase their zygotes in a fibrous capsule that is made even more durable by the addition of calcium salts, thereby producing calcareous shells. Additional details of protective barriers are in Chapter 4.

Larvae—Free-Living Embryos

The diversity of amphibian larval morphology equals the diversity of adult stages. Most larvae feed during their free-living developmental period; however, some do not eat and depend upon the yolk stores of the original ovum.

Caecilian and salamander larvae resemble adults in general appearance and anatomical organization (Fig. 2.4).

The transition (metamorphosis) from embryonic larva to nonembryonic juvenile is gradual with only minor reorga-FIGURE 2.3 The concept of heterochrony can be applied to a wide nization. In contrast, the anuran larva (tadpole) undergoes variety of traits. The New World microhylid, Dermatonotus muelleri, a major reorganization during its metamorphosis from has a tiny head relative to its body and, because other New World micro-embryo to juvenile because the tadpole is anatomically hylids are similar, truncation of head development likely occurred in an ancestor to the clade of New World microhylids. (Luis Gasparini) different from the juvenile and adult.

Salamanders

Frogs

Aquatic/pond types

Ambystoma tigrinum Sphaenorhynchus orophilus Aquatic/stream types

Eurycea bislineata Babina holsti

Terrestrial/direct development types *Plethodon glutinosus Eleutherodactylus nubicola* FIGURE 2.4 Body forms of some amphibian larvae arranged by habitat type.

With few exceptions, larvae of the three amphibian the centrally located body is spherical, and a muscular groups are aquatic. All share anatomical characteristics tail provides the thrust that results in tadpole movement.

associated with an aquatic existence. They have thin, frag-Functional limbs do not appear until late in larval life ile skin consisting of two or three epidermal layers. The and then only the hindlimbs are visible externally. The skin is heavily vascularized owing to its role as a major front limbs develop at the same time as the hindlimbs, respiratory surface, a role shared with the gills. All but they are enclosed within the operculum and emerge amphibian larvae develop pharyngeal slits and external only at metamorphosis.

gills—usually three pairs that project from the outside of The general tadpole body form has been modified into the pharyngeal arches. The external gills persist and func-hundreds of different shapes and sizes, each adapted to a tion throughout the larval period in salamanders, basal specific aquatic or semiterrestrial habitat and feeding anurans, and caecilians. In tadpoles of neobatrachian behavior. This diversity has been variously partitioned.

frogs, external gills are resorbed and replaced by internal In the 1950s, Dr. Grace Orton recognized four basic body gills, which are lamellar structures on the walls of the pha-plans; her morphotypes defined the evolutionary grade of ryngeal slits. All larvae have lidless eyes and large, non-tadpoles and to some extent their phylogenetic relation-valvular nares. They have muscular trunks and tails for ships. Another approach is to examine the relationship undulatory swimming, and the tails have dorsal and ven-between tadpole morphology and ecological niches. One tral fins. The skeleton is entirely or mainly cartilaginous.

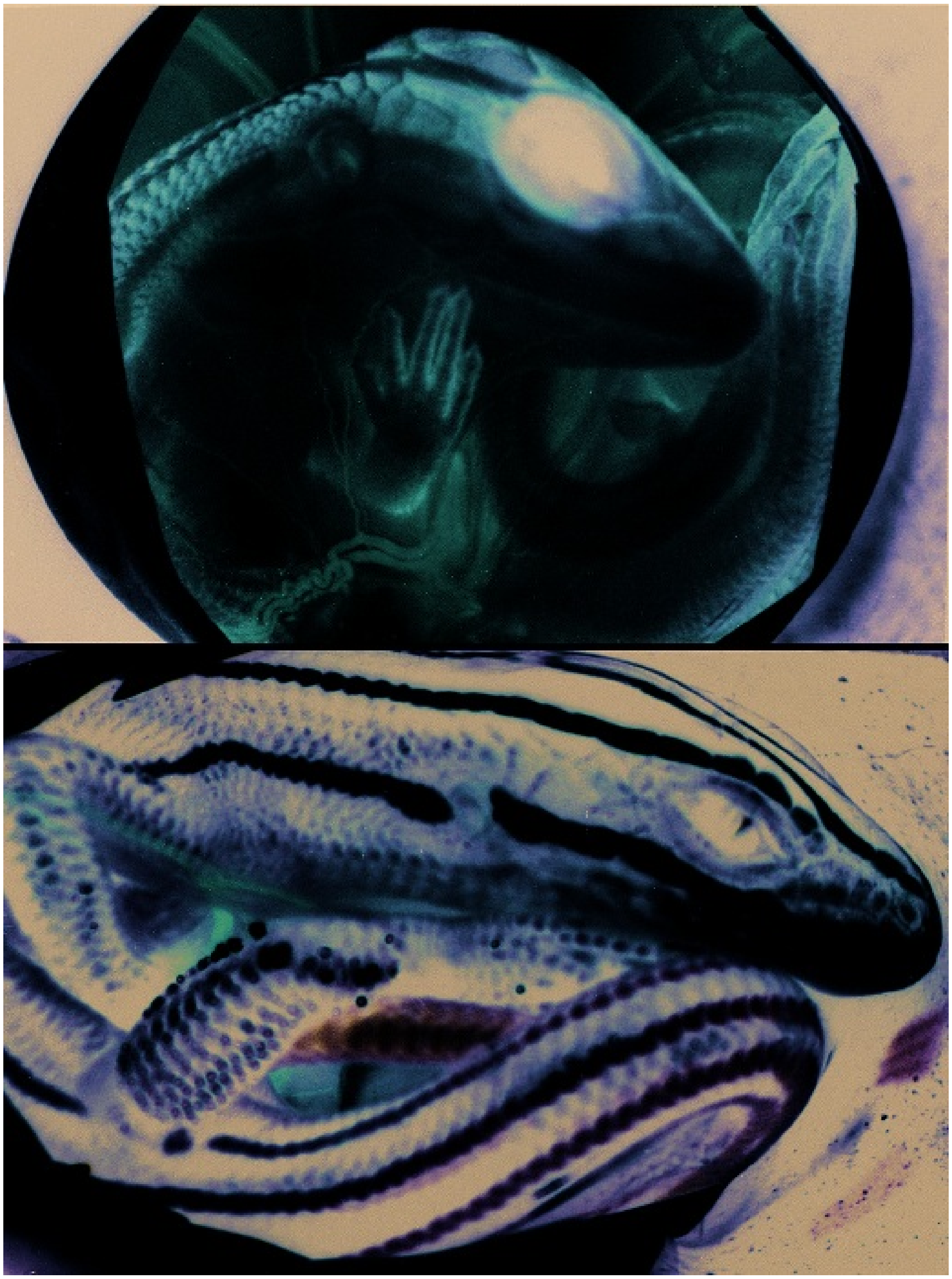
such an analysis defined 18 guilds based on ecomorphol-All have well-developed lateral line systems.

ogy, which, with their subcategories, included 33 body Caecilian and salamander larvae are miniature adult types. Although morphotypes can define adaptive zones replicates, differing mainly by their smaller size, pharyn-of tadpoles, they do not necessarily reflect phylogenetic geal slits and gills, tail fins, a rudimentary tongue, and relationships because considerable convergence has occurred.

specialized larval dentition. In contrast the body plan of Both classifications emphasize external, oral, and pharyngeal the anuran tadpole bears little similarity to the adult's.

morphology.

In general, tadpoles are well designed for consuming food Most tadpoles have a large, fleshy disc encircling their and growing; the most salient feature of the body is a large mouth. Depending on the manner of feeding and the type coiled intestine. Mouth and eyes are situated anteriorly, of food, the oral disc ranges in position from ventral



(suctorial, to anchor in swift water and scrape food off rocks) to dorsal (grazing on surface film in calm water) and in shape from round to dumbbell. The margin of the disc is variously covered with papillae, and these have a variety of shapes. Their actual function remains uncertain, although chemosensory, tactile, and current detection are some possibilities. Tadpoles lack teeth on their jaws; instead many tadpoles have keratinous jaw sheaths and parallel rows of keratinous labial teeth on the oral disc above and below the mouth. The labial teeth are not homologous with teeth of other tetrapods. The jaw sheaths cut large food items into smaller pieces; the rows of labial teeth act as scrapers or raspers to remove food from rocks and plant surfaces. The oral–pharyngeal cavity is large. Its structures trap and guide food into the esophagus, as well as pump water through the cavity and across the gills. The gills are initially visible externally, but at hatching or shortly thereafter, an operculum grows posteriorly from the back of the head to fuse to the trunk, enclosing the gills and the developing forelimbs. To permit water flow, a single spiracle or pair of spiracles remains open on the posterior margin of the operculum. Because the operculum covers the gill region, the head and body form a single globular mass. Adhesive glands are transient structures present near the mouth in early embryonic stages at the time of hatching. The glands secrete a sticky substance that tadpoles use to adhere to their disintegrating egg mass or to some structure in the environment. Because of the FIGURE 2.5 Reptiles are tightly coiled inside of eggs prior to hatching.

Embryos of Plestiodon fasciatus inside of eggs. Developmental stage 39

fragility of the newly hatched larvae, adherence provides (upper); stage 40 (lower). (James R. Stewart) stability for the larva until the oral disc and tail musculature develop fully and locomotion becomes possible.

natural selection over generations of females. Nevertheless, the abiotic and biotic environments are extremely variable, Life in an Eggshell

and eggs and their enclosed embryos must tolerate and respond to these varying conditions. A few examples illus-The eggshell protects the reptile embryo, but in so doing, it trate the breadth of nesting environments and egg–embryo imposes special costs on embryo growth and physiology.

physiological responses.

An amphibian larva can grow to near adult size before Temperature tolerances of embryos lie typically within metamorphosing, although most do not. A reptile in an egg-the tolerance range of the juveniles and adults of their spe-shell cannot grow in size within the shell but must undergo cies, but because the rate of development is temperature complete development prior to hatching. By folding and dependent and eggs lack the mobility to avoid extremes, curling, a reptile embryo can attain surprising lengths, but exposure to extremes is likely to be fatal. At low tempera-it is still smaller than would be possible outside of a shell tures, development slows down and hatching is delayed, (Fig. 2.5). Determinants of offspring size are complex and resulting in emergence at suboptimal times or embryos discussed elsewhere (see “Life Histories” in Chapter 5).

that never complete development. At high temperatures, Most reptile hatchlings are, however, heavier than the mass the embryo’s metabolism increases exponentially so that of the original ovum. Metabolism of the yolk uses water yolk stores are depleted before development is completed, absorbed through the shell, and the embryo grows beyond and of course, either extreme can be directly lethal by the original ovum.

damaging cells and/or disrupting biochemical activity.

Just as temperature, water availability, and gas exchange The selection of protected oviposition sites potentially avoids affect the physiological processes of juveniles and adults, the extremes of temperature and provides a stable tempera-they also have the greatest impact on developing eggs. Eggs ture environment. But temperatures do fluctuate within and are not laid randomly in the environment; females select among nests, and in some reptiles with temperature-depen-sites that offer the greatest potential for egg and hatchling dent sex determination, skewed sex ratios among hatchlings survival. Oviposition site selection has been honed by can result (see Chapter 5).

Moisture is no less critical for the proper development During much of larval life, growth is emphasized over and survival of reptile embryos than for amphibians; how-morphogenesis. Morphogenesis is greatest in the early ever, amphibians typically require immersion in water, stages and then slows for caecilian and salamander larvae; whereas immersion of most reptile eggs results in suffoca-frog larvae similarly undergo major development changes tion of embryos. Embryos do not drown; rather, the sur-in their early stages, but they also display distinct struc-rounding water creates a gaseous-exchange barrier at the tural changes throughout larval life (Fig. 2.6). Larval life shell–water interface, and the small amounts of gases that span is variable—from less than 20 days in some spade-cross are inadequate to support cellular metabolism. The foot (frogs in the family Scaphiopodidae) populations to Australian sideneck turtle Chelodina rugosa avoids this several years in other frogs and salamanders. The duration dilemma, even though females lay their eggs in submerged is species specific and genetically fixed, but not rigidly so.

nests. Once the eggs are laid, development stops. Develop-Metamorphosis marks the beginning of the end of larval mental arrest typically occurs in the gastrulation phase, life; once begun, metamorphosis usually proceeds rapidly.

and embryogenesis begins only when the water disappears Rapidity is necessary to reduce the transforming amphi-and the soil dries, permitting the eggs and/or the embryos bian's exposure to predation or other potential stresses to respire. The relative availability of water affects the rate when it is neither fully aquatic nor fully terrestrial.

of development and absolute size of the hatchlings, at least Metamorphosis is initiated internally by the hormone in turtles. Chrysemys picta eggs in high-moisture nests thryroxine, but environmental factors can initiate early hatch sooner and produce larger hatchlings than those thyroxine release if a larva has completed certain mor-from nests with lower moisture. Developmental abnormal-phogenic events. For example, crowding, reduced food ities can also result if hatchlings experience dehydration as or oxygen, drying of water bodies, or increased predation embryos.

can result in thyroxine release. Although thyroxine and Adequate gas exchange is an unlikely problem for spe-its derivatives promote metamorphosis, they do not opercies that lay or attach their eggs openly in cavities or crevices ate alone. The thyroid is present early in larval life, but (e.g., many geckos), but for the majority of reptiles that bury its secretory activity is apparently inhibited by corticoid their eggs, adequate gas exchange can be critical. Changes in hormones, such as corticosterone. Furthermore, prolactin soil permeability affect the diffusion of air, drier soils having is abundant in early larval stages and makes the body the highest diffusion rates and wet soils the lowest. Similarly, tissues insensitive to thryroxin. When these inhibitions the friability of soils and associated aspects of particle size are removed, the thyroid secretes thyroxin, effecting and adhesiveness influence the movement of gas through transformation.

the soil. In selecting a nesting site, a female must balance her ability to dig an egg chamber with the presence of adequate moisture to prevent desiccation and yet not retard Hatching and Birth gaseous diffusion, as well as a multitude of other factors.

In amphibians, the timing of hatching depends upon the CHANGING WORLDS—METAMORPHOSIS,

life history. For those species with larvae, hatching occurs HATCHING, AND BIRTH

early in embryogenesis typically at Gosner stage 17, and for those species with direct-developing embryos, hatching Metamorphosis

occurs at the completion of development. Direct-developing embryos do not pass through a major metamorphic Metamorphosis in amphibians is the transformation of the event. Exit from the egg in either situation requires penetra-larva to a miniature adult replicate, and usually from an tion of the gelatinous egg capsules. The actual hatching aquatic to a terrestrial or semiterrestrial lifestyle. It signals mechanism is known only for a few species, but because the completion of embryogenesis. Some developmental these all share “hatching” glands on the snout and head processes, such as maturation of gonads, continue through of the larvae, the mechanism is probably common to most the juvenile stage, but the major structural and physiolog-other amphibians.

These

glands

secrete

proteolytic

ical features are in place at the conclusion of metamorpho-enzymes that weaken and dissolve the capsules, allowing sis. Metamorphosis is nearly imperceptible in caecilians the larva or juvenile to escape. Froglets in the genus and salamanders but dramatic in frogs (Table 2.3). Anuran Eleutherodactylus are assisted by an egg tooth, a bicuspid larvae require major structural and physiological reorgani-structure located on the upper lip. Stage 15 embryos use zation because of the striking differences between the lar-the structure to slice through the tough outer egg capsules.

val and the juvenile/adult stages. Change does not occur The structure sloughs off within two days after hatching.

all at once but gradually, each step leading to next level Birth, whether from an intrauterine or extrauterine situa-of transformation. Unlike insect pupae, metamorphosing tion and whether as a larval or juvenile neonate, appears tadpoles remain active, capable of avoiding predators to be triggered by a combination of maternal hormonal and environmental stresses.

activity and embryonic/fetal secretions.

TABLE 2.3 Anatomical Changes in Frogs and Salamanders Accompanying Metamorphosis.

FROGS

SALAMANDERS

Buccal region

Major remodeling

Slight remodeling

Oral disc with papillae and keratinous denticles and beak disappears

Jaws elongate, enlarging mouth, and teeth develop Teeth change from bicuspid to monocuspid Buccal musculature reorganized

Tongue muscles develop

Tongue muscles develop

Pharyngeal region

Remodeling with shortening of the pharynx Gills and pharyngeal slits disappear Gills and pharyngeal slits disappear Rearrangement of aortic arches

Rearrangement of aortic arches

Modification of hyoid and segments of the branchial skeleton for

Modification of hyoid and segments of the branchial skeleton for tongue support tongue support

Viscera

Lung development completed

Lung development completed

Stomach develops

Digestive tube modified slightly

Reduction of intestine and change of digestive epithelium Reduction of pancreas

Pronephros kidney disappears

Pronephros kidney disappears

Skin

Number of epidermal cell layers increases Number of epidermal cell layers increases Pigmentation and pattern change

Pigmentation and pattern change

Skeleton

Ossification moderate to strong

Ossification slight to moderate

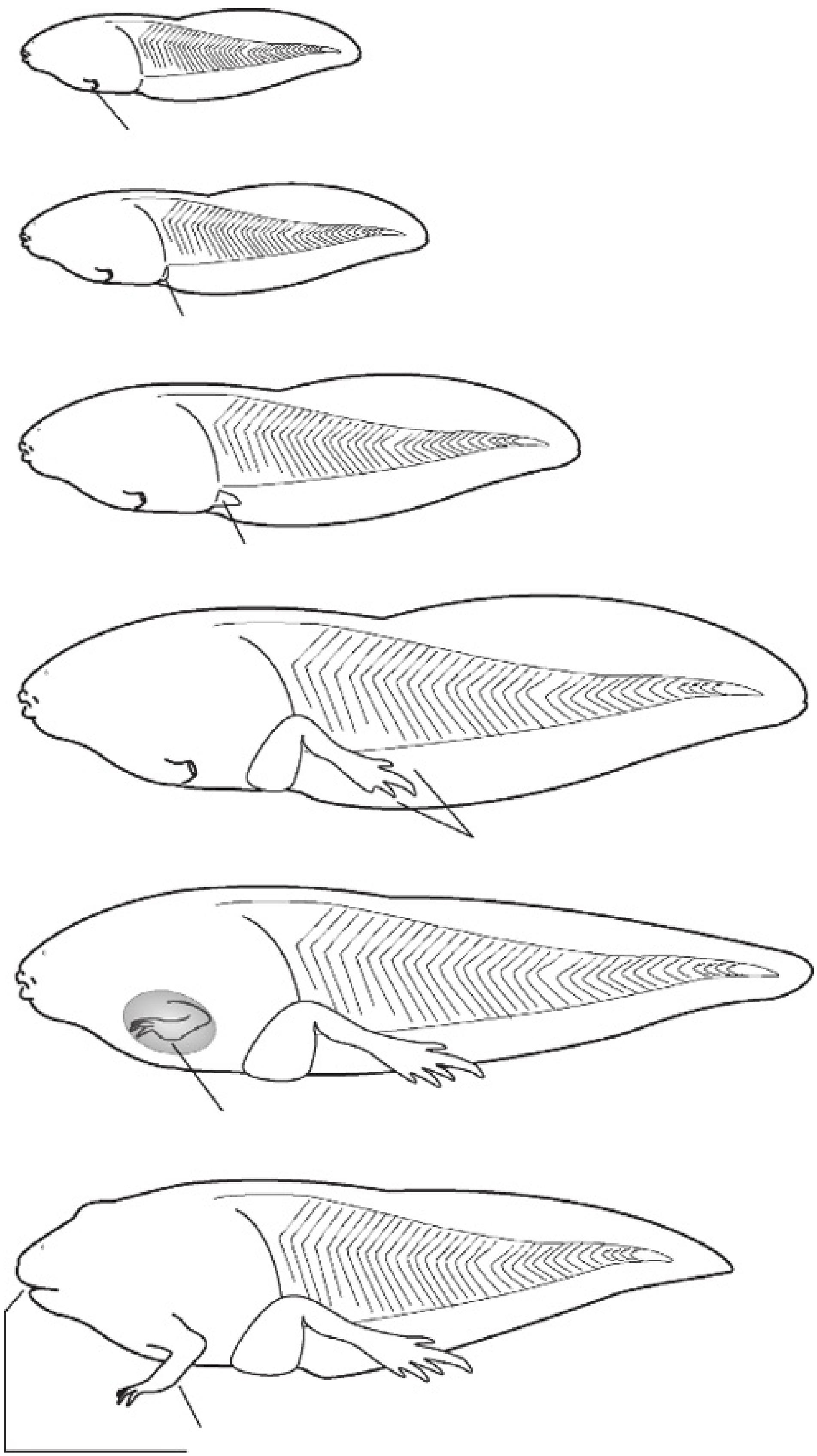
Major remodeling of cranial skeleton Little change in cranial skeleton

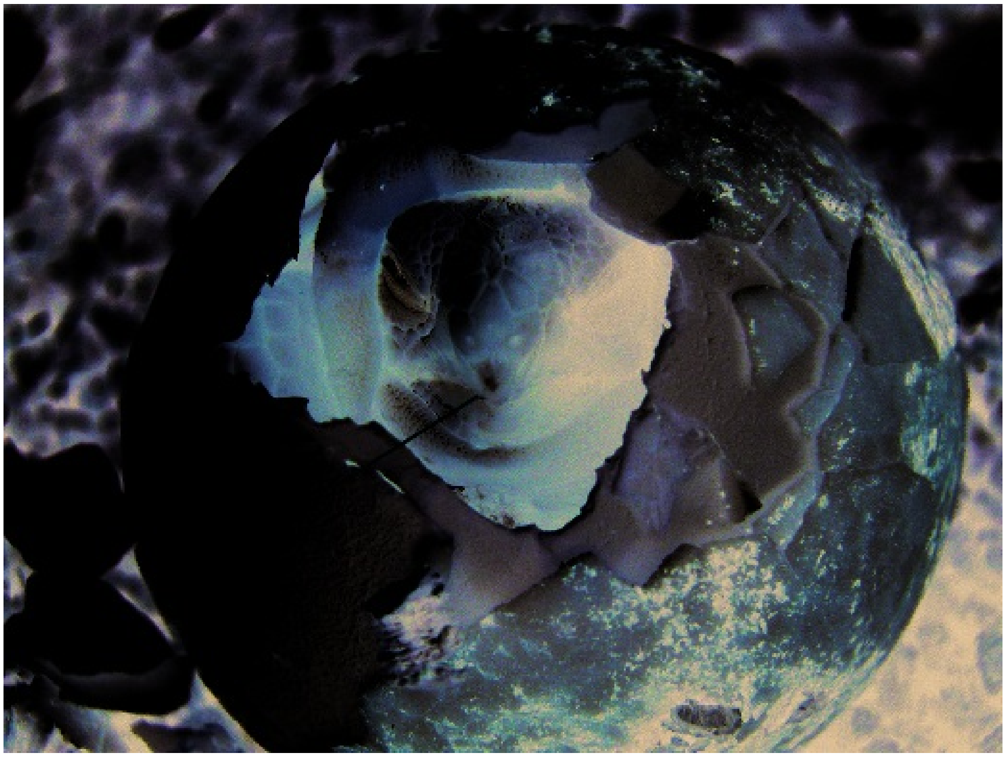
Loss of tail; development of urostyle Sense organs

Protrusion of eyes with development of eyelids Protrusion of eyes with development of eyelids Remodeling of eye and growth of eye muscles Development of stapes in middle ear Note: These structural changes represent only a portion of anatomical changes occurring during metamorphsis.

Source: Hourdry and Beaumont, 1985.

Birth in reptiles appears to be triggered largely by mater-is a keratinous protuberance, the egg caruncle, which slices nal hormonal activity, although a maternal–fetal feedback through the encasing layers (Fig. 2.7). Crocodylian and turtle mechanism plays an essential role in the female's hormonal embryos extract calcium from the eggshell during their cycles. Hatching in reptiles requires the penetration of the embryogenesis, and this weakening of the eggshell makes amnionic membranes and the eggshell. Reptiles use a projec-it easier to rupture. Squamates presumably lost the caruncle tion on the tip of the snout to break through these two enclo-and replaced it with an egg tooth that projects outward from sures. In turtles, crocodylians, and Sphenodon, the projection the premaxillary bone. Hatching can be extended, requiring





Stage 25

spiracle developed

Stage 26

rear limb bud

length < 1/2 of diameter

Stage 30

Egg tooth

rear limb bud length

is twice diameter

Stage 36

FIGURE 2.7 Photograph of the egg of a Geochelone sulcata just beginning to hatch. The arrow points to the emerging egg tooth as it begins to slice through the leathery shell. (Tim Colston) GROWTH three toes distinct

Stage 41

Growth is the addition of new tissue in excess of that required for the replacement of worn-out or damaged tissue. As a cellular process, growth rate in ectotherms depends on temperature, slowing and ceasing as temperature declines; excessive temperature also slows or halts growth because maintenance and metabolic costs exceed forelimb ready to emerge

energy procurement. Growth is influenced by the avail-Stage 43

ability and quality of food. In this respect, ectotherms have an advantage over endotherms by ceasing to grow during food shortages and renewing growth when food becomes available. This is one reason why reptiles and amphibians often persist in large numbers in extreme environments such as deserts when resources become low, either seasonally or as the result of extended drought. Metabolic demands forelimb emerged and

of endothermy in mammals and birds render them vulnera-larval mouthparts gone ble to starvation when resources are low.

FIGURE 2.6 Selected larval stages of a typical anuran. Stage terminol-Growth occurs primarily in the embryonic and juvenile ogy from Gosner (1960).

stages of amphibians and reptiles. Embryonic growth usually is proportionately greater than juvenile growth, because embryos possess abundant, high-quality energy several hours to a day for complete emergence, but can also resources in the form of the yolk that require little energy be rapid, with near synchrony of hatching among eggs in the expenditure for acquiring and processing. Juveniles and same nest. A few turtles have delayed emergence, hatching free-living amphibian larvae face variable food supplies, in autumn but not emerging from the nest until spring. This often with low energy content, and must expend energy situation alerts us to the possibility that hatching and nest to obtain and process food, while simultaneously avoiding emergence are potentially separate events in other reptile predation and environmental hazards. From hatching or species as well. Generally, parents are not involved in the birth, most reptiles and amphibians will increase 3-to hatching and emergence process. Nevertheless, parental cro-20-fold in length, but some species may increase over codylians aid their young during hatching and emergence 100-fold in mass. Growth may or may not continue indef-and some skinks (New World

Mabuya) remove embryonic initely throughout life; unlike mammals and birds, in membranes from neonates when they are born. The possibil-which growth slows dramatically or stops at sexual matu-ity exists that many more species aid in the hatching and rity (determinate growth), sexually mature amphibians and emergence process but are simply difficult to observe and reptiles generally continue growing, giving the impression thus are unreported.

that growth is indeterminate.

Mechanics of Growth

indeterminant growth

large

All tissues grow during juvenile life, although the rate varies among tissues. Growth can be measured by changes in overall size, most often in length. Mass is more variable determinant growth

owing to numerous factors, such as hydration, gut contents, and reproductive state, each of which can change Size

an animal's weight without changing its overall length.

Skeletal growth is the ultimate determinant of size because sexual

the skeleton is the animal's supportive framework. Skele-maturity tal elements of amphibians and reptiles usually lack epi-small physes and grow by apposition, a process in which one layer forms on top of another. Because of these attributes, young old

extended growth is possible and leads to the assumption of indeterminate growth in these animals. Other reasons for assuming that indeterminate growth occurs are the large large

sizes of individuals in some species and the continuation of growth long after sexual maturity.

Both indeterminate (attenuated) and relatively determinate (asymptotic) growth exist in amphibians and reptiles, but the evidence for one or the other is lacking for most Size

species (Fig. 2.8). Indeterminate growth may be less frequent than commonly assumed. Adult size for most sexual

species lies within a narrow range, suggesting that growth maturity

ceases. Older adults of some reptilian species have fused small

epiphyses. The two growth patterns in natural populations are difficult to distinguish because a narrow adult size young old

range may indicate only that high mortality truncates the Age

growth or size potential of the species or population.

FIGURE 2.8 General growth pattern trends for amphibians and reptiles.

Whatever the end point, juvenile growth is rapid and Top: comparison of indeterminant and determinant growth. When growth is relatively indeterminant, constant growth rate as a juvenile is followed slows as sexual maturity is approached. Most juvenile by slower, but continuous growth once sexual maturity is reached. When growth fits one of two curvilinear patterns: parabolic growth is determinant or asymptotic, a sigmoid pattern during juvenile growth, which may begin rapidly and remain rapid for stages is followed by slower growth after sexual maturity and finally cur-most of juvenile life, or sigmoid growth, which is initially tailment of growth. Bottom graph: hypothetical growth for an ectotherm slow, becomes rapid, and then slows again. Both patterns in a seasonal environment follows a pattern of rapid growth during equable seasons and greatly reduced or no growth during adverse seasons.

show a plateau associated with maturity, a result of the reallocation of energy resources to reproduction. Individual growth curves are not smooth (Fig. 2.8), particularly in ectotherms. Growth proceeds fast or slow depending Age

on the abundance of food, and it may halt for months at a time in species in seasonal environments, including trop-The length of time an individual lives is not as critical as ical wet and dry seasons. Growth may proceed ratchetlike the time required to reach the major life-history events of for the first few years of sexual maturity because energy hatching or birth, sexual maturity, and reproductive senil-is alternately allocated to reproduction and then to growth.

ity. Reproductive periodicity, the time interval between Ratchetlike growth curves also result from seasonal varia-episodes of the production of offspring, is another critical tion in resource availability.

age-related aspect of an individual’s life history. In amphi-The ultimate size of an individual depends on its bians with a larval stage, two intervals are critical: genetic potential, size at hatching, abundance and quality embryogenesis within the egg and larval period to meta-of food during juvenile growth, and its sex. Heredity morphosis. All of these events are regularly subjected to determines the potential range of growth rate and size or selection within a population, and the modal condition age at sexual maturity. Beginning with hatchlings of the within a population can shift.

same size, species, and sex, faster growth or longer juve-Age at sexual maturity ranges from 4 to 6 months nile life yields larger adults. These factors and others (Arthroleptis poecilonotus, an artholeptid frog) to 7 years yield the variations in adult size within and between (Cryptobranchus, hellbender salamander) for amphibians species.

and from 2 to 4 months (Anolis poecilopus, a polychrotine

lizard) to 40þ years (Chelonia mydas, green seaturtle) for may live more than half a century (e.g., Geochelone reptiles. These marked extremes reflect differences in gigantea). Annual or biennial species have little time for adult size only in part, because not all small species growth, so these species typically are small; the opposite mature so quickly or large ones so slowly (Table 2.4).

is not true for the long-lived species. Although many Age of maturity is a compromise among many variables long-lived species are large, some, such as the yucca ghost-on which selection may operate to maximize an indivi-lizard, Xantusia vigilis, are tiny yet long-lived. Often small-dual’s contribution to the next generation. Maturing and bodied long-lived reptiles or amphibians have secretive reproducing quickly is one strategy, but small body size lifestyles.

reduces the number and/or size of offspring and smaller adults tend to experience higher predation. Maturing later at a larger body size permits the production of more and/or INTEGUMENT—THE EXTERNAL

larger offspring but increases the probability of death prior ENVELOPE

to reproducing, and may yield a smaller total lifetime out-put of offspring. The resulting diversity in size and age The skin is the cellular envelope that forms the boundary at sexual maturity, number and size of offspring, and the between the animal and its external environment, and as frequency of reproduction illustrate the numerous options such, serves multiple roles. Foremost are its roles in sup-molded by natural selection for attaining reproductive port and protection. The skin holds the other tissues and success.

organs in place, and yet it is sufficiently elastic and flexi-Longevity often indicates a long reproductive life span ble to permit expansion, movement, and growth. As a proof an individual or species. The reproductive life span of tective growth. As a proof an individual of species. The reproductive life span of tective barrier, it prevents the invasion of microbes and some species (e.g., Uta stansburiana) is a single reproduc-inhibits access by potential parasites, resists mechanical tive season, and most individuals disappear from the invasion and abrasion, and buffers the internal environ-population within a year of hatching. Longevity in a few ment from the extremes of the external environment. The surviving individuals of Uta stansburiana can exceed skin also serves in physiological regulation (e.g., heat and 3 years in natural populations. For other species the repro-osmotic regulation), sensory detection (chemo-and mecha-ductive life span can be a decade or longer, and individuals noreception), respiration, and coloration.

TABLE 2.4 Natural Longevity of Select Amphibians and Reptiles.

Taxon

Adult size (mm)

Age at maturity (mo)

Maximum age (mo)

Cryptobranchus alleganiensis

330

84

300

Desmognathus quadramaculatus

73

84

124

Eurycea wilderae

34

48

96

Anaxyrus americanus

72

36

60

Lithobates catesbeianus

116

36

96

Chrysemys picta

119

72

360

Geochelone gigantea

400

132

840Æ

Trachemys scripta

195

50

288

Sphenodon punctatus

180

132

420þ

Aspiciscelis tigris

80

21

94

Gallotia stehlini

120

48

132þ

Uta stansburiana

42

9

58

Diadophis punctatus

235

32

180þ

Pituophis melanoleucus

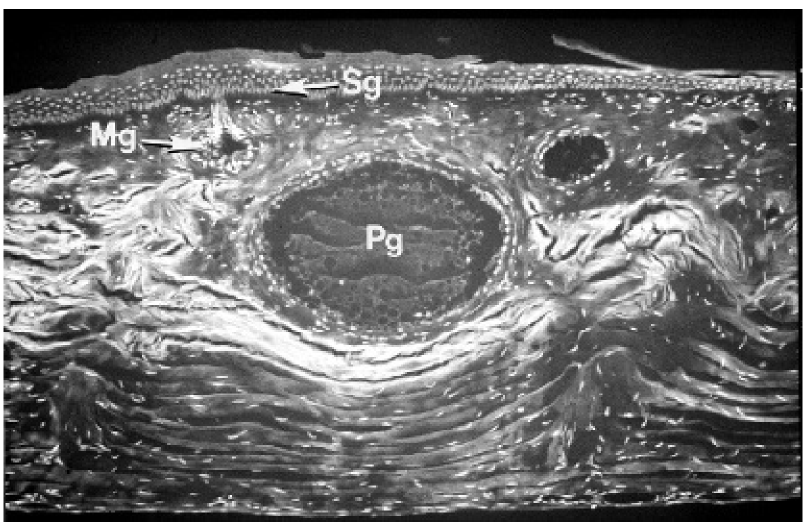
790

34

180þ

Note: Body size is for females at sexual maturity (mm, snout-vent length except carapace length for turtles); age of maturity for females (months); maximum age of either sex (mo).

Sources: Salamanders – Ca, Peterson et al., 1983; Dq, Bruce, 1988b; Organ, 1961; Ew, Bruce, 1988a. Frogs – Aa, Kalb and Zug, 1990; Lc, Howard, 1978. Turtles – Cp, Wilbur, 1975; Gg, Bourne and Coe, 1978; Grubb, 1971; Ts, Frazer et al., 1990. Tuataras – Sp, Castanet et al., 1988. Lizard – At, Turner et al., 1969; Gs, Castanet and Baez, 1991; Us, Tinkle, 1967; Medica and Turner, 1984. Snakes – Dp, Fitch, 1975; Pmd, Parker and Brown, 1980.



example, scutes are the same as shields, but scansors are Epidermis

scales or lamellae beneath the digits that allow geckos to S. spongiosum

Epidermis

cling to nonhorizontal surfaces. All reptilian scales are keratinized epidermal structures, but those of the lepidosaurs are not homologues of crocodylian and turtle scales.

S. spongiosum

Scales commonly overlap in squamates but seldom do in Dermis

crocodylians and turtles.

S. compactum

Dermis

Two patterns of epidermal growth occur. In crocodylians and turtles, the cells of the stratum germinativum divide continuously throughout an individual's life, stopS. compactum ping only during hibernation or torpor. This pattern is shared with most other vertebrates, from fishes to mam-FIGURE 2.9 Amphibian skin. Cross section through the ventral skin of a marine toad Rhinella [Bufo] marina. Abbreviations: Mg, mucus gland; mals. A second pattern, in which growth is discontinuous Pg, poison or granular gland; Sc, stratum compactum; Sg, stratum germi-but cyclic, occurs in lepidosaurs (see the later section nativum; Ss, stratum spongiosum.

"Ecdysis"). Upon shedding of the outer epidermal sheath (Oberhautchen), the germinative cells enter a resting phase Amphibian skin consists of an external layer, the epider-with no mitotic division. The renewal phase begins with the mis, which is separated from the internal layer, the dermis, synchronous division of the germinative cells and the dif-by a thin basement membrane (Fig. 2.9). The epidermis is ferentiation of the upward-moving epithelium into two dis-typically two to three cell layers thick in larvae and five to tinct layers separated by a narrow layer of cell secretions.

seven layers thick in juvenile and adult amphibians. The The surface of each reptilian scale is composed entirely innermost layer of cells (stratum germinativum) divides con-of ß-keratin, and the interscalar space or suture is composed tinuously to replace the worn outer layer of epidermal cells.

of a-keratin. This distribution of keratin produces a durable The outer cell layer is alive in larvae, but in most juveniles and protective scale surface with junctures between the and adults, cells slowly flatten, keratinize, and die as they scales that allow flexibility and expansion of the skin.

are pushed outward. This layer of dead, keratinous cells Although the preceding pattern is typical, the scales on (stratum corneum) shields the inner layers of living cells the limbs of some turtles have surfaces composed of from injury. The dermis is a thicker layer, containing many a-keratin, and in softshell and leatherback turtles, the sur-cell types and structures, including pigment cells, mucous face of the shell is composed of a-keratin. In most of the and granular glands, blood vessels, and nerves, embedded hard-shelled turtles, the scutes and sutures contain only in a connective tissue matrix (Fig. 2.9). The innermost layer ß-keratin. The two-layered epidermis of the lepidosaurs of dermis is a densely knit connective tissue (stratum com-has an a-keratin inner layer and a ß-keratin Oberhautchen.

pactum), and the outer layer (stratum spongiosum) is a looser An anomaly of special interest is the occurrence of matrix of connective tissue, blood vessels, nerve endings, individual snakes that are nearly scaleless in several spe-glands, and other cellular structures. In caecilians and sala-cies of colubrids and viperids. Only the labial and ventral manders, the stratum compactum is tightly linked with the scales are usually present. The remainder of the skin is a connective tissue sheaths of the muscles and bones. In con-smooth sheet of soft, keratinous epidermis. Genetically, trast, much of the body skin is loosely attached in frogs.

scalelessness appears to be a simple Mendelian homozy-The skin of reptiles has the same cellular organization gous recessive trait.

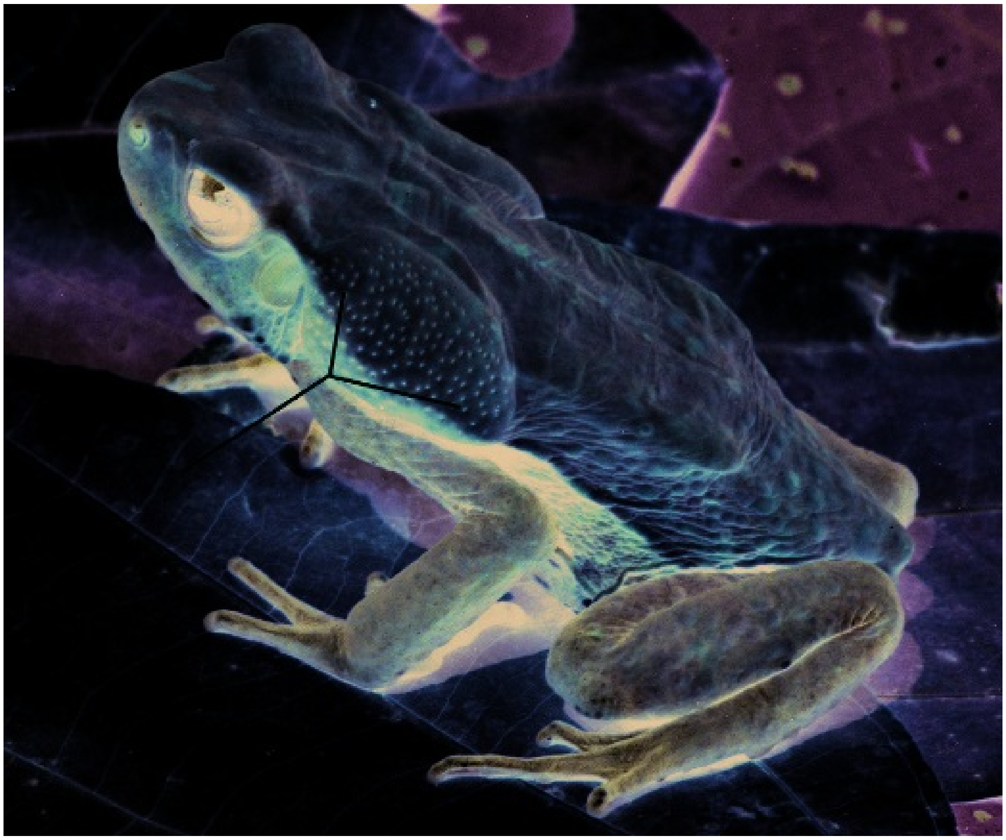
as in amphibians. Notably, the epidermis is thicker with numerous differentiated layers above the stratum germinativum. Differentiation produces an increasingly thick, INTEGUMENTARY STRUCTURES

keratinous cell membrane and the eventual death of each cell. This basic pattern is variously modified among reptil-Amphibian Glands and Skin ian clades and occasionally among different parts of the Structures

body of the same individual. Reptiles uniquely produce ß-keratin as well as a-keratin, which they share with other Amphibians have several types of epidermal glands. Mucous vertebrates. ß-keratin is a hard and brittle compound, and granular (poison) glands occur in all postmetamorphic whereas a-keratin is elastic pliable.

(i.e., juvenile and adult) amphibians and are numerous and On all or most of the body, skin is modified into scales.

widespread on the head, body, and limbs (Fig. 2.9). Both The scales are termed plates, scutes, shields, laminae, types are multicellular, flask-shaped glands with the bul-lamellae, scansors, or tubercles, depending upon the taxo-bous, secretory portion lying within the stratum spongiosum nomic group, the size and shape of the scales, and the of the dermis; their narrow necks extend through the epider-location of the scales on the body. Some names are intermis and open on its surface. Although occurring over the changeable, whereas others refer to specific structures. For entire body, the glands are not evenly distributed; their role their role



determines their density and location. Mucous glands are the this annular pattern can be complicated by the development most abundant; about 10 of them are present for every gran-of secondary and tertiary grooves; the secondary ones ular gland. The mucous glands are especially dense dorsally, appear directly above the myosepta. The warts, papillae, and they continuously secrete clear, slimy mucus that main-flaps, tubercles, and ridges in frogs and salamanders can tains a thin, moist film over the skin. The granular glands be aggregations of glands or simply thickenings in the tend to be concentrated on the head and shoulders. Presum-underlying dermis and epidermis.

ably, predators that attack these vulnerable parts of the body Although amphibians lack epidermal scales, they do would be deterred when encountering poisonous or noxious have keratinous structures. Clawlike toe tips of pipid secretions produced by the glands. The granular glands are frogs, spades of scaphiopodid frogs, and rough, spiny skin often aggregated into macroglands, such as the parotoid of some frogs and salamanders are keratinous. These glands of some frogs and salamanders (Fig. 2.10). Usually structures persist year-round. Other keratinous structures these macroglands contain more complex individual

Other keratinous structures these macroglands contain more complex individual glands.

are seasonal and usually associated with reproduction.

Larvae have a greater variety of epidermal glands.

Many male salamanders and frogs have keratinous nuptial Most are single-celled (unicellular), although many can pads on their thumbs at the beginning of the mating sea-be concentrated in a single region. For example, the hatch-son; some even develop keratinous spines or tubercles on ing glands are clustered on the dorsal forepart of the head.

their arms or chests. At the end of the mating season, these Unicellular mucous glands are widespread and secrete a specialized mating structures are typically shed, and they protective mucous coat over the surface of the living epi-redevelop in subsequent breeding seasons.

dermis. This mucous coat also serves as a lubricant to Dermal scales exist only in caecilians, although not in enhance the flow of water over the larva when swimming.

all species. These scales are flat, bony plates that are buried Merkel and flask cells are scattered throughout the larval deeply in pockets within the annular grooves. Whether epidermis, but they are not abundant in any region. Their these scales are homologues of fish scales remains uncer-functions are uncertain. Merkel cells might be mechanore-tain. Some frogs, such as Ceratophrys and Megophrys, ceptors, and flask cells may be involved in salt and water have osteoderms (bony plates) embedded in or immediately balance.

adjacent to the dermis. In some other species of frogs, the The skin of amphibians ranges from smooth to rough.

dorsal skin of the head is compacted and the connective Some of the integumentary projections are epidermal, but tissue of the dermis is co-ossified with the skull bones, most involve both the epidermis and the dermis. Integu-a condition known as exostosis.

mentary annuli of caecilians and costal grooves of salamanders match the segmentation of the axial musculature and vertebral column. Each primary annulus and each costal REPTILIAN SCALES, GLANDS, AND SKIN

groove lies directly over the myosepta (connective tissue STRUCTURES sheet) between the muscle masses; thus, the number of annuli equals the number of trunk vertebrae. In caecilians, Scales of crocodylians, turtles, and some lizards (e.g., anguids, cordylids, scincids) are underlain by bony plates, called osteoderms or osteoscutes, in the dermis. Organization of osteoderms aligns with organization of the dermis.

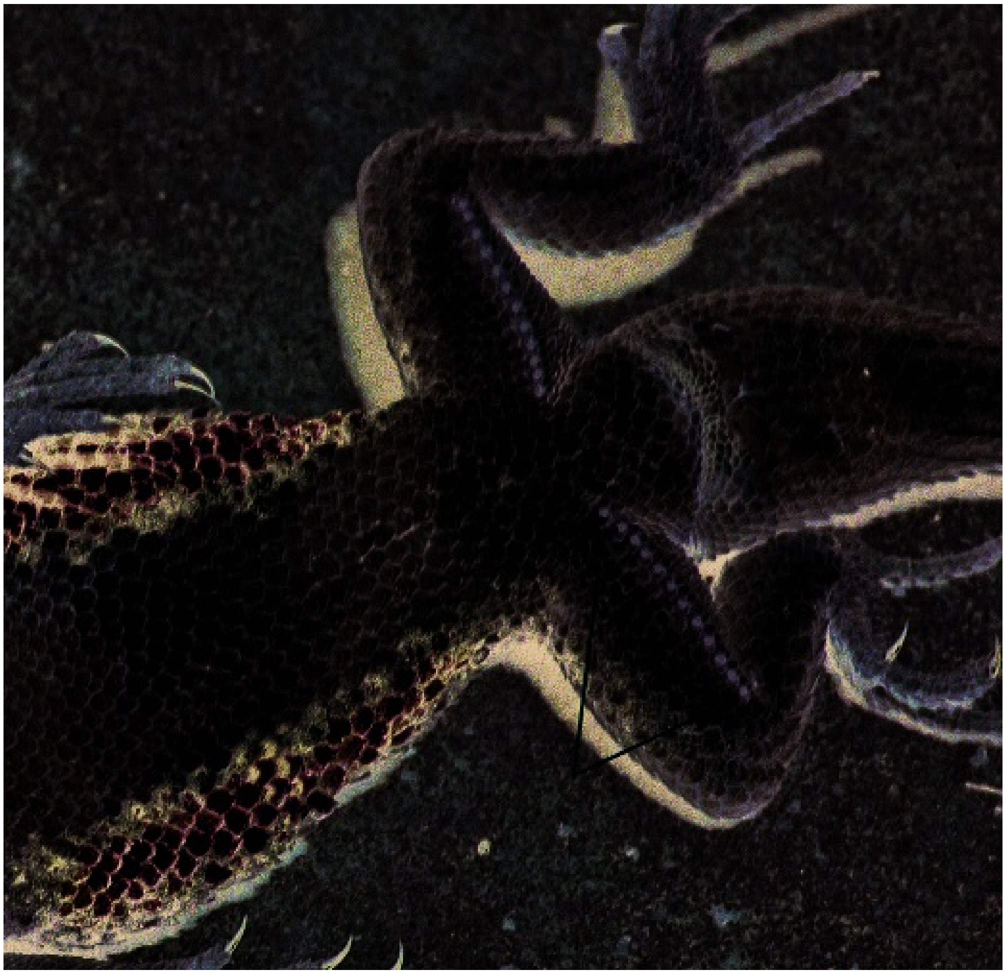
The outer layer of osteoderms is spongy, porous bone; the inner layer is compact, dense bone. Usually osteoderms are confined to the back and sides of the animal and attach loosely to one another in symmetrical rows and columns to permit flexibility while maintaining a protective bony armor. In crocodylians and a few lizards (Heloderma), the osteoderms fuse with the dorsal skull elements, forming a rigid skull cap. In turtles, the carapace (upper shell) arose from the fusion of osteoderms with vertebrae and Paratoid gland

ribs dorsally, whereas the plastron (lower shell) arose from the fusion of osteoderms and the sternum ventrally.

Reptiles have a variety of skin glands. Although common over the body, the multicellular glands are typically small and inconspicuous. Their secretions are mainly lipid-and wax-based compounds that serve as waterproofing, surfactant, and pheromonal agents.

FIGURE 2.10 The tropical toad Rhaebo guttatus has enlarged paratoid Aggregations of glandular tissues occur in many rep-glands behind the head as well as many other glands over the body surface.

Secretions from the paratoid glands are toxic. (Janalee P. Caldwell) tiles. Musk or Rathke's glands are present in all turtles



except tortoises (Testudinidae) and in some emydid outermost layer is formed of hard ß-keratin. The claws turtles. These glands are usually bilaterally paired and lie form either as full keratinous cones, as in crocodylians within the bridge between the top and bottom shells, open-and turtles, or as partial cones, as in lepidosaurs. The ing to the outside through individual ducts in the axilla upper and lower jaw sheaths of turtles are also keratinous and inguinal region or on the bridge. Male tortoises have structures and replace the teeth as the cutting and crushing a mental gland just behind the tip of the lower jaw. Both surfaces. Hatchling turtles, crocodylians, and Sphenodon male and female crocodylians have paired mandibular have an egg caruncle on the snout to assist in hatching.

and cloacal glands. The occurrence of large glands is more A dozen or more types of small, epidermal sense erratic in lepidosaurs. Some geckos and iguanians have a organs occur in reptiles, particularly in lepidosaurs. Most series of secretory pores on the underside of the thighs are barely visible, appearing as tiny pits or projections.

and pubis (Fig. 2.11). Each pore arises from the center These epidermal structures are not shed during the slough-of an enlarged scale and produces a waxy compound con-ing cycle. Presumably, most of these structures respond to taining cell fragments. These femoral and precloacal tactile stimuli; however, the presence of a light-sensitive (pubic) pores do not open until the lizards attain sexual region on the tail of a seasnake suggests a broader range maturity and often occur only in males. They may function of receptors and sensitivities. These organs are often con-as sexual scent glands. Snakes and some autarchoglossan centrated on the head but are also widespread on the body, lizards have paired scent glands at the base of the tail; each limbs, and tail.

gland opens at the outer edge of the cloacal opening. These saclike glands release copious amounts of semisolid, bad-smelling fluids. For some species, the fluid may serve in ECDYSIS

defense, whereas in other situations, they may function for sexual recognition. Other glandular aggregations occur Adult amphibians shed their skin in a cyclic pattern of sev-but are limited to a few reptiles. For example, a few Austra-eral days to a few weeks. This shedding, called ecdysis, lian geckos have specialized squirting glands in their tails, sloughing, or molting, involves only the stratum corneum and some marine and desert species of turtles, crocody-and is commonly divided into several phases. At its sim-lians, and lepidosaurs have salt glands.

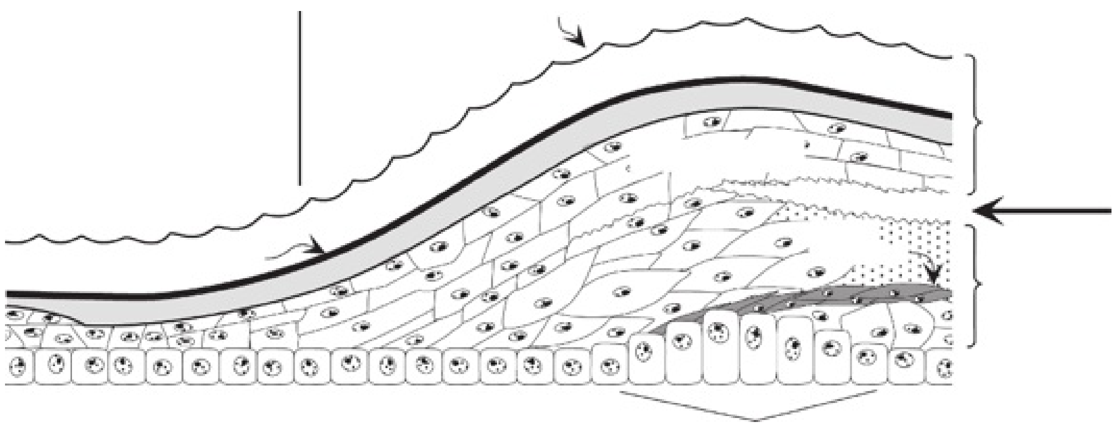
plest, the shedding cycle consists of epidermal germination Specialized keratinous structures are common in rep-and maturation phases, pre-ecdysis, and actual ecdysis.

tiles. All limbed species with functional digits have claws, These phases are controlled hormonally, although timing which are keratinous sheaths that encase the tips of the and mechanisms differ between species and amphibian terminal phalanges. The sheaths have three layers. The groups. The stratum germinativum produces new cells that move outward and upward in a conveyer-belt-like fashion as new cells are produced beneath them. Once these new cells lose contact with the basement membrane, they cease dividing and begin to mature, losing their subcellular organelles. Pre-ecdysis is signaled by appearance of mucous lakes between the maturing cells and the stratum corneum. The lakes expand and coalesce, and the cellular connections between the dead cells of the stratum corneum and the underlying, maturing cells break. Externally, the skin commonly splits middorsally first over the head and then continues down the back. Using its limbs, the frog or salamander emerges from the old skin, which is often consumed. During the pre-ecdytic and/or the ecdytic phase, the epidermal cells beneath the mucous lakes complete their keratinization and die.

The shedding process of larval amphibians is not well known. In the mudpuppy Necturus maculosus and probably in most other larvae, the skin is shed as single cells or in small pieces. The shed skin is not keratinized and Femoral pores

may be alive when shed. The epidermal cells mature as they are pushed to the surface, but keratinization is not part of maturation.

In reptiles, different epidermal organizations and FIGURE 2.11 Femoral pores of the male of the lizard Sceloporus undulatus are located along the posterior edge of the underside of the growth patterns produce different shedding or slough-thighs. They appear as lines of black spots. (Laurie Vitt) ing patterns. In the epidermis of crocodylians and the



nonshell epidermis of turtles, cell growth is continuous and the portions of the outer surface of the skin are shed continuously in flakes and small sheets. Depending on species, the scutes of hard-shelled turtles are either retained or shed seasonally. When retained, successive scutes form a flattened pyramid stack, because an entire new scute develops beneath the older scute at the beginning of each growing season. Scute growth is not confined to the margins, although each new scute is thickest there and much compressed beneath the older scutes.

The shedding pattern in lepidosaurs is more complex and intimately tied to the unique epidermal growth pattern. In the tuataras and most lizards, the skin is shed in large patches, whereas in snakes the skin is usually shed as a single piece. But in all lepidosaurs, the sequence of epidermal growth and shedding is identical (Fig. 2.12).

FIGURE 2.13 Anolis punctatus shedding its skin. Note that the old skin During the resting stage, the epidermis has a basal germi-separates in several places from the new skin (Laurie Vitt).

native layer of cells, a narrow band of a precursor cells, a thin meso-layer of mucus and other cell secretions, and COLORATION externally the beginnings of an outer-generation layer capped by the Oberhautchen. The resting stage ends as The color of amphibians is affected by the presence of pig-cell proliferation and differentiation begins in the outer-ment cells (chromatophores) in the dermal layer of the skin.

generation layer. Then the germinative cells begin to Three classes of chromatophores are melanophores, irido-divide. As each newly formed layer of cells is pushed phores, and xanthophores. The primary pigment in melano-upward and outward by cell division below them, the cells phores is eumelanin, which imparts black, brown, or red differentiate and produce the inner-generation layer. This coloration. Pigments in iridophores are purines such as gua-inner-generation layer forms the precursor of the scales nine; these cells reflect light because of pigment-containing (outer-generation layer) for the next epidermal cycle.

organelles arranged in stacks. Xanthopores impart yellow, As the Oberhautchen nears completion, the outer-generation orange, or red coloration because they contain pteridine layer separates from the inner layer and is shed, comple-pigments. In addition to containing different pigments, ting the shedding or sloughing cycle (Fig. 2.13). This each of the three cell types is structurally different. The three cycle is repeated at regular intervals when food is abundant.

classes of chromatophores are arranged as a unit and produce This growth–shedding (renewal) phase requires about an animal’s external coloration (Fig. 2.14). For example, the 14 days. The resting phase may last from a few days to blue color of iridophores combined with the yellow color of many months.

xanthophores produces a green-colored skin.

Oberhautchen

β-layer

Resting

Renewal

α-layer

outer

generation

lacunar tissue

layers

Oberhautchen

β-layer

meso layer

meso layer

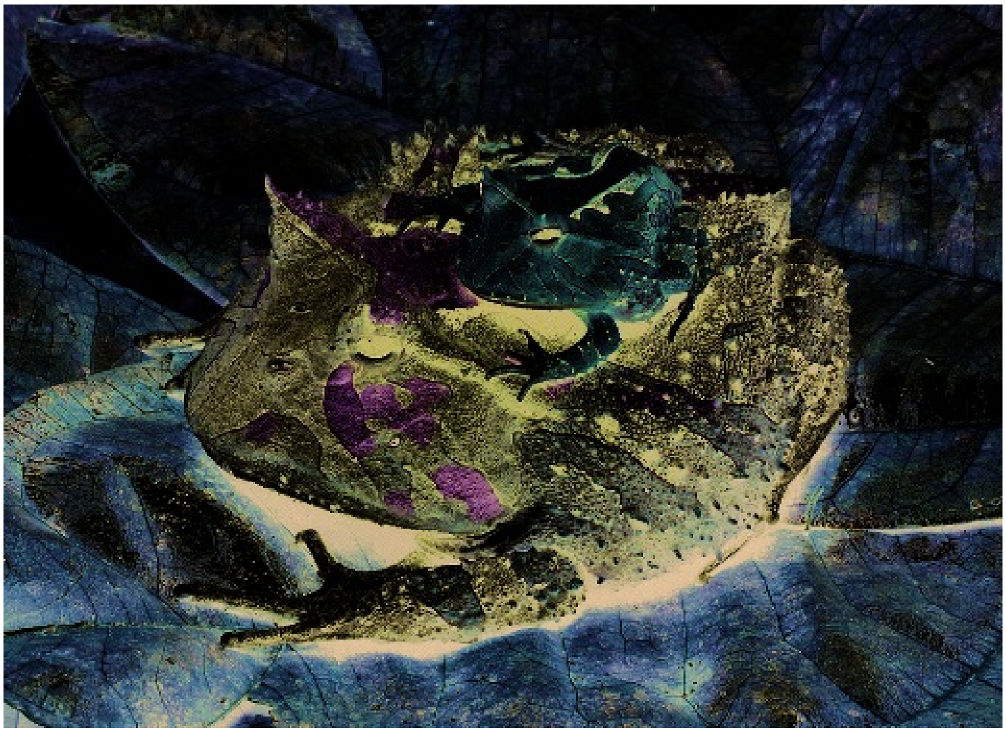
inner

generation

layers

stratum germinativum

FIGURE 2.12 Diagram of the sequential cellular changes during a single shedding cycle in squamate epidermis. Adapted from Landmann (1986).



DERMAL CHROMATOPHORE UNIT

Epidermis

Basal lamina

xanthophore

iridiphore

Dermis

melanophore

FIGURE 2.14 The arrangement of chromatophores in amphibian skin, called the dermal chromatophore unit.

The unit consists of xanthophores, which give yellow, orange, or red coloration; the iridophores, which reflect light and cause bright colors; and the basal melanophores, which have dendritic processes that extend between the xanthophores and the iridophores.

Melanophores have a central cell body with long, epidermal growth, the melanophores send out pseudopodia attenuated processes radiating outward. Melanophores that transfer melanin into the differentiating keratocytes.

occur individually in the epidermis or as part of the The melanin-bearing keratocytes occur in the ß-layer dermal chromatophore unit. Epidermal melanophores are of crocodylians, iguanian lizards, and snakes, and in the common in larvae and are often lost or reduced in their a-and ß-layers in many other lizards.

number at metamorphosis. The dermal chromatophore unit The second type of cell that produces color is the chro-contains a basal melanophore, an iridophore, and a terminal matophore, which is structurally similar to that in amphi-xanthophore. Dendritic processes of the melanophore bians. Different types of chromatophores are stacked in extend upward and over the iridophore, which is then over-the outer portion of the dermis. A single layer of xantho-lain by a xanthophore (Fig. 2.14). The color produced by phores (= lipophores and erythrophores) lies beneath the the unit depends largely upon the color of pigment in the xanthophore and the reflectivity of the iridophore. Melanophores are largely responsible for lightening or darkening of the color produced in the other two chromatophores.

Color changes can occur quickly, in less than a minute, by dispersal or reduction of the eumelanin within the melanophores’ processes. Increased eumelanin darkens the observable color of the skin, while reduced eumelanin allows colors produced by the iridophores and xanthophores to predominate. Slow color changes may take weeks to months and occur when pigment concentration increases or decreases within the chromatophores or when pigment is in adjacent cells. Short-term color changes are controlled by hormonal or nervous stimulation. Some species have spec-tacular coloration and patterns that aid in crypsis (Fig. 2.15).

patterns that aid in crypsis (Fig. 2.15).

Reptiles generally have two types of color-producing FIGURE 2.15 Frog skin contains a variety of pigments that often result cells. Melanophores are scattered throughout the basal in bizarre intricate patterns, as in this Amazonian Ceratophrys cornuta layers of the epidermis. During the renewal phase of (Janalee P. Caldwell).

basal membrane of the epidermis. Beneath the xanthro-Most elements from these two cranial skeletons appear phores are two to four layers of iridophores (= guano-first as cartilage. Cartilaginous precursors define the posi-phores and leukophores), and at the bottom are large tion of the later developing bony element. Bone formed by melanophores. This organization may represent the gen-replacement of cartilage is called replacement or endo-eral pattern for all reptiles that change color, because chondral bone. The dermocranium contains the roofing stacked chromatophores are absent in some species that elements that lie external to the chondro-and splanchno-do not change color. The presence, density, and distribu-cranial elements. These roofing elements have no cartilag-tion of chromatophores within each layer vary within inous precursors; instead, ossification centers develop in an individual and among species to produce the different the dermis and form dermal or membrane bones.

colors and color patterns.

All three crania are represented by numerous skeletal elements in fish and in the fish ancestors of amphibians.

SKELETON AND MUSCLES—SUPPORT,

The earliest amphibians showed a loss of elements from each of the crania and a firmer articulation of the remain-MOVEMENT, AND FORM

ing elements. The reduction has continued in modern tetrapod clades, which have lost additional, but often dif-The evolutionary transition from a fishlike ancestor to ferent, elements in each group. Fewer elements have been amphibians was accompanied by major reorganizations lost in the caecilians, in which the skull is a major digging within the musculoskeletal system. As ancestral tetrapods tool and must remain sturdy and firmly knit, often by the shifted their activities from an aquatic to a terrestrial envi-fusion of adjacent elements (see Fig. 15.1).

ronment, the buoyant support of water disappeared, and the In extant amphibians, much of the chondrocranium pull of gravity required a strengthening of the vertebral col-remains cartilaginous throughout life (Fig. 2.16). Only umn to support the viscera. Simultaneously, these ancient the sphenoethmoid

(orbitosphenoid

in

salamanders),

tetrapods were shifting from undulatory locomotion to which forms the inner wall of the orbit, and the fused limbed locomotion. The new functions and demands on prootic and exoccipital, which form the rear of the skull, the musculoskeletal system required a more tightly linked ossify. Within the skull proper, the bony elements of the vertebral column, elaboration of the limbs and girdles, splanchnocranium are the stapes (ear) and the quadrate and modification of the cranium for capture and ingestion (upper jaw). Meckel's cartilage forms the core of the man-of terrestrial food. As in amphibians, the reptilian musculo-dible (lower jaw), and ossification in its anterior and pos-skeletal system is adapted primarily for terrestrial limbed terior ends form the mentomeckelian bone and articular, locomotion, and some species are secondarily modified respectively. The dermal bones form the major portion for aquatic or terrestrial limbless locomotion. With the of the adult skull, linking the various cranial elements exception of turtles, reptiles retain considerable lateral flex-and forming a protective sheath over the cartilaginous ele-ure of the body, and only in archosaurs does dorsoventral ments, the brain, and the sense organs. The skull is roofed flexure become an important component of locomotion.

from anterior to posterior by the premaxillae, nasals, fron-Each extant amphibian group has had a long and inde-tals, and parietals; each side of the skull contains the max-pendent evolutionary history. Many structural differences illa, septomaxilla, prefrontal, and squamosal. Dermal appeared during this long divergence, and these differ-bones also sheath the skull ventrally, creating the primary ences are nowhere more apparent than in the composition palate (roof of mouth). The palate consists of vomers, and organization of the musculoskeletal system. Similarly, palatines, pterygoids, quadratojugals, and a parasphenoid, the long independent evolution of each reptilian group is which is the only unpaired dermal bone in the amphibian strongly evident in all aspects of their musculoskeletal skull. The dermal bones of the mandible are the dentary, system. This great diversity permits us to present only a angular, and prearticular, which encases Meckel's carti-general survey of he musculoskeletal systems of amphi-lage. Teeth occur commonly on the premaxillae, maxillae, bians and reptiles.

vomers, palatines, and dentaries.

The jaws of vertebrates arose evolutionarily from the HEAD AND HYOID

first visceral or branchial arch. The second visceral, hyomandibular, arch supported the jaws and bore gills, and The cranial skeleton of vertebrates contains elements from the third and subsequent visceral arches comprised the three units: the chondrocranium, the splanchnocranium, major gill arches. Remnants of these arches remain in and the dermocranium. The chondrocranium (neurocra-modern amphibians. The jaws consist mostly of dermal nium) comprises the skeleton surrounding the brain and bones; only the mentomeckelian, articular, and quadrate the sense organs, that is, the olfactory, optic, and otic cap-are bony remnants of the first arch. The quadrate becomes sules. The splanchnocranium is the branchial or visceral part of the skull proper, and the dorsalmost element of the arch skeleton and includes the upper and lower jaws, the hyomandibular arch becomes the stapes for transmission hyobranchium, and the gill arches and their derivatives.

of sound waves from the external eardrum, the tympanum,

Epicrionops petersi nasal

premaxillary

maxillary—

vomer

frontal

squamosal

palatine

maxillary—

quadrate

pterygoid

pterygoid

palatine

os basale

squamosal

quadrate

parietal

premaxillary

pseudoangular

os basale

pseudodentary

Salamandra salamandra premaxillary

premaxillary

nasal

vomer

prefrontal

orbitosphenoid

vomer

parietal

maxillary

maxillary

squamosal

frontal

orbito—

parietal

sphenoid

pterygoid

pterygoid

dentary

quadrate

squamosal

prearticular

quadrate

prootic—

squamosal

articular

prootic—

parasphenoid

exoccipital

exoccipital

Gastrotheca walkeri premaxillary

premaxillary

sphenethmoid

maxillary

sphenethmoid

maxillary

palatine

fronto—

frontoparietal

parietal

nasal

prootic

pterygoid

pterygoid

maxillary

dentary

quadratojugal

angulosplenial

squamosal

prootic

prootic

exoccipital

quadratojugal

exoccipital

quadratojugal

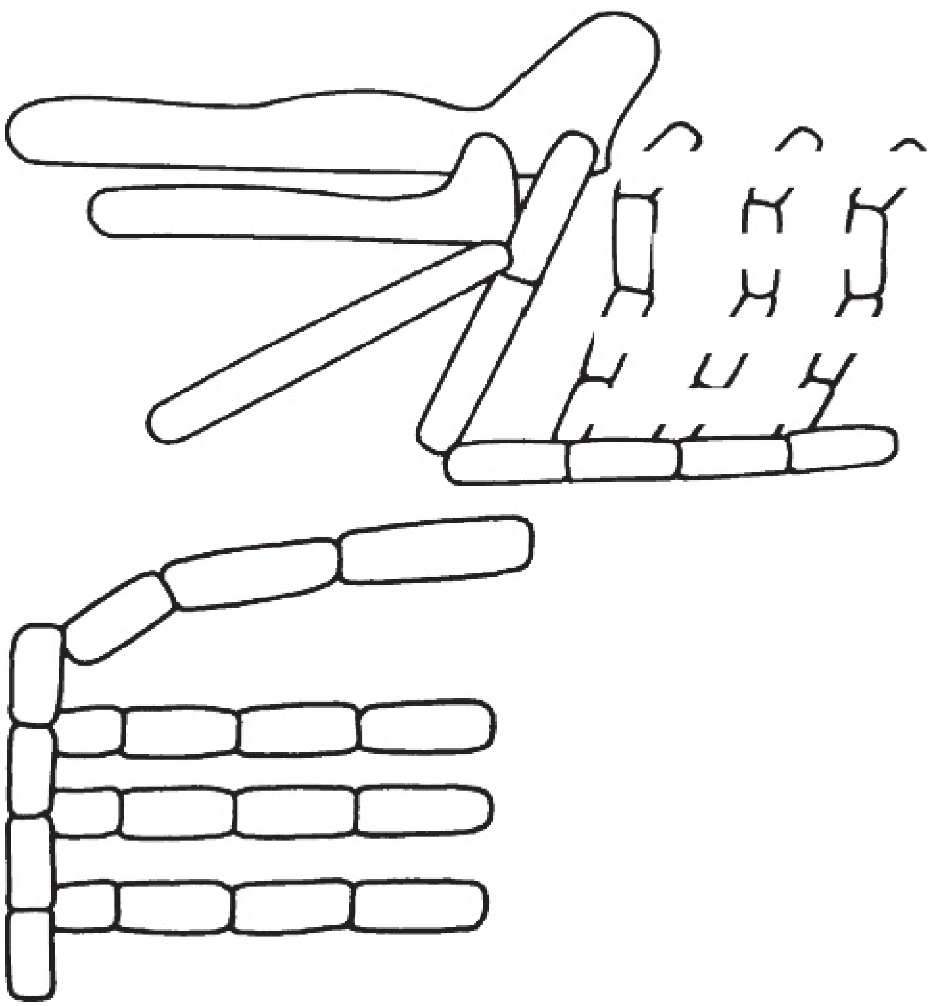
squamosal

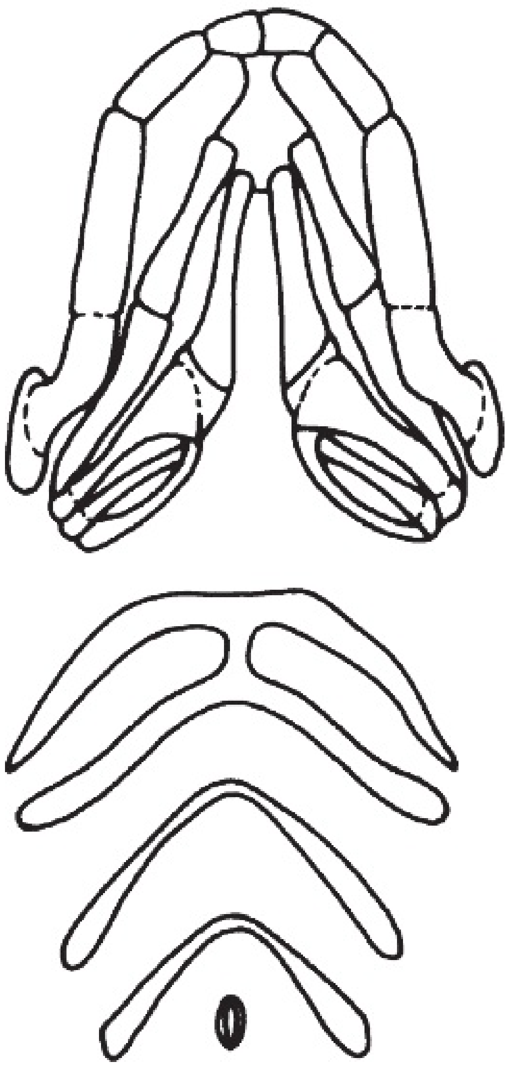
parasphenoid

FIGURE 2.16 Cranial skeletons of representatives of the three clades of extant amphibians. Dorsal, lateral, and ventral views (left to right) of the caecilian Epicrionops petersi, the salamander Salamandra salamandra, and the frog Gastrotheca walkeri. Reproduced, with permission, from Duellman and Trueb (1986).

to the inner ear. The ventral portion of the second arch adults. Some elements from the more posterior visceral persists as part of the hyoid apparatus. The subsequent arch become structural supports in the glottis, larynx, two to four visceral arches may persist, at least in part, and trachea.

as gill arches in larvae and in some gilled adults (e.g., Pro-The composition and architecture of the hyoid is teidae), and also as elements of the hyoid in juveniles and highly variable within and between each group of living





amphibians. In all, the hyoid lies in the floor of the mouth dorsal surface of the mandible close the mouth, and those and forms the structural support for the tongue. In some that attach to the lateral and ventral surface of the mandi-species, the components of the hyoid can be traced accu-ble open the mouth. The muscles that function in respira-rately to their visceral arch origin; in others species, their tion and swallowing form the floor of the mouth, throat, origin from a specific arch element is uncertain. The hyoid and neck. These muscles move and support the gills and/

elements in primitive salamanders retain an architecture or the hyoid and the tongue.

similar to that of the visceral arches of fishes, but with In reptiles, the anterior portion of the chondrocranium the loss of arch elements (Fig. 2.17). In more advanced remains cartilaginous, even in adults, and consists mainly salamanders, the number of hyoid elements is further of continuous internasal and interorbital septa and a pair reduced. The hyoid remains cartilaginous in caecilians of nasal conchae that support olfactory tissue. Between without segmentation of hyoid arms into individual ele-the eyes and ears, the chondrocranium ossifies as the basi-ments. The anuran hyoid is a single cartilaginous plate sphenoid, and further posteriorly, the basioccipital, a pair with two to four processes and has little resemblance to of exoccipitals, and the supraocciptal bones develop below its visceral arch precursor.

and behind the brain (Fig. 2.18). The occipital elements The cranial musculature contains one functional group encircle the foramen magnum, the site at which the spinal for jaw movement and another for respiring and swallow-cord exits the skull. Below the foramen magnum, the ing. The jaw muscles fill the temporal area of the skull, exoccipitals and the basioccipital join to form a single extending from the area of the parietal, prootic, and squa-occipital condyle, which bears the articular surface mosal to the mandible. The muscles that attach to the between the first cervical vertebra, the atlas, and the skull.

Generalized vertebrate hyobranchial skeleton lateral view

dorsal view (left side removed)

hyomandibular

ceratohyal

hyomandibular

basihyal

ceratobranchial

chondrocranium

epibranchial

pharyngobranchials

hyobranchial

pharyngobranchial

palatoquadrate

basibranchial I

epibranchials

basibranchial II

ceratobranchials

basibranchial III

Meckel’s cartilage

hyobranchials

ceratohyal

basihyal

basibranchial IV

basibranchial I

basibranchial II

basibranchial III

basibranchial IV

Cryptobranchus

lchthyophis

basihyal

basibranchial I

ceratohyal

hyohyal

basibranchial I

ceratohyal

hyobranchial

ceratobranchial I

hyomandibular

ceratobranchial II

ceratobranchial III & IV

ceratobranchial

arytenoid cartilage

FIGURE 2.17 The hyobranchial skeleton of a typical vertebrate, the salamander Cryptobranchus (dorsal view), and the caecilian Ichythyophis (ventral view). Reproduced, with permission, from Duellman and Trueb, 1986.

Pseudemydura umbrina nasal

premaxillary

maxillary

maxillary

prefrontal

postorbital

frontal

vomer

frontal

prefrontal

palatine

nasal

parietal

postorbital

pterygoid

squamosal

basisphenoid

maxillary

parietal

prootic

jugal

pterygoid

basioccipital

quadrate

quadrate

exoccipital

supra—

basioccipital

occipital

squamosal

opisthotic

supraoccipital

Alligator sinensis premaxillary

maxillary

premaxillary

maxillary

nasal

parietal

squamosal

frontal

quadrate

palatine

lacrimal

prefrontal

quadratojugal

lacrimal

nasal

articular

prefrontal

premaxillary

jugal

jugal

maxillary

surangular

ectopterygoid

frontal

angular

dentary

pterygoid

postorbital

jugal

parietal

quadratojugal

quadrate

quadratojugal

squamosal

basioccipital

quadrate

Ctenosaura pectinata premaxillary

premaxillary

maxillary

nasal

vomer

lacrimal

prefrontal

prefrontal

frontal

postorbital

parietal

palatine

squamosal

jugal

premaxillary

palatine

prootic

frontal

ectopterygoid

maxillary

quadrate

pterygoid

pterygoid

basisphenoid

jugal

postorbital

pterygoid

parietal

prootic

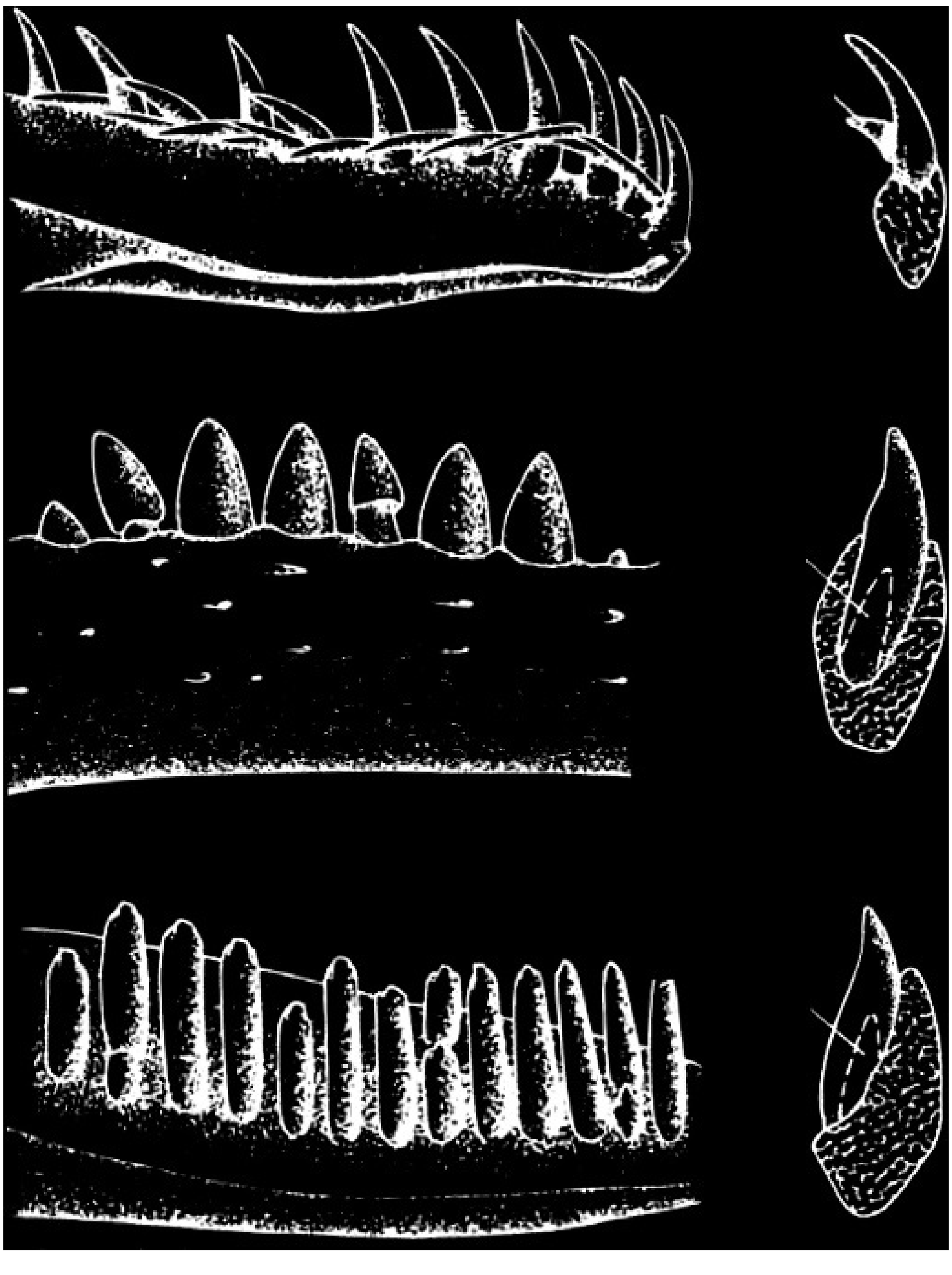
quadrate

squamosal

quadrate

basioccipital

FIGURE 2.18 Cranial skeletons of representatives of the three clades of living reptiles. Dorsal, lateral, and ventral views (left to right) of the turtle Pseudemydura umbrina, the crocodylian Alligator sinensis, and the lizard Ctenosaura pectinata. Adapted from Gaffney (1979), Iordansky (1973), and Oelrich (1956), respectively.



Regions of each otic capsule remain cartilaginous, Acrodont

Replacement

although much of the capsule becomes the epiotic, prootic, tooth

and opisthotic bones.

The stapes of the middle ear is a splanchnocranial element, as are the quadrate and the epipterygoid; the latter is small in lizards and turtles and is lost in snakes and archosaurs. The quadrate is a large bone on the posterolat-eral margin of each side of the skull. It bears the articular surface for the lower jaw. On the mandible, the articular bone provides the opposing articular surface and is the Thecodont

only splanchnocranial element of the lower jaw. The rep-Replacement tilian hyoid arch is reduced and consists of a large mid-tooth ventral plate, usually with three processes that extend upward and posteriorly.

Dermal bones compose the major portion of the reptilian skull and mandible, forming over and around the endo-chondral bones. From anterior to posterior, the roof of the dermocranium contains the nasals, prefrontals, frontals, and parietals, all of which are paired. The upper jaws, the premaxillae, and the maxillae join the roofing bones directly.

Pleurodont

Replacement

The cheek and temporal areas contain a postorbital, post-tooth frontal, jugal, quadratojugal, and squamosal bone on each side. The primary palate or roof of the mouth consists of premaxillae and maxillae anteriorly, and a median vomer that is bordered laterally by the palatines and posteriorly by the pterygoids and occasionally a parasphenoid. When a secondary palate forms as in crocodylians, it derives largely from the premaxillae and maxillae. A few other dermal bones, FIGURE 2.19

for example, the septomaxilla and the lacrimal, are present Reptile teeth can sit on top of the jaw (acrodont), embedded in the jaw (thecadont), or on the side of the jaw (pleurodont).

in some extant reptiles. The jugals, the quadratojugals, pre-Tooth location is one of the many important taxonomic characters used to frontals, postfrontals, and squamosals are absent individually separate major taxa. Adapted from Kardong, 2006.

or in various combinations in some taxa.

The mandible or lower jaw contains numerous paired arcade composed of parietals, squamosals, postorbitals, dermal bones including dentaries, splenials, angulars, jugals, and quadratojugal lacks openings (anapsid).

surangulars, coronoids, and prearticulars (Fig. 2.18). Only Although the lack of openings in the quadratojugal has the dentary bears teeth, and in the upper jaw, only the max-historically placed turtles with anapsids, this condition illa, premaxilla, palatine, and pterygoid bear teeth. Teeth appears to be secondarily derived from a diapsid ancestor can be absent on one or more of these teeth-bearing bones.

in turtles (Fig. 2.20). In the typical diapsid skull, the tem-In turtles, teeth are entirely absent; their cutting and crush-poral area has two openings called fenestrae, an upper one ing functions are performed by the keratinous jaw sheaths.

between the parietal and the postorbital–squamosal, and a Typical reptilian teeth are cone-shaped and arranged lower one between the squamosal and jugal–quadratoju-in a single, longitudinal row. This basic shape has been gal. Most living turtles have emarginated temporal variously modified. For example, the teeth are laterally arcades, leaving a small arch of bone behind each eye.

compressed and have serrated edges in some herbivo-Only a few turtles, such as the seaturtles, retain a nearly rous lizards and are elongated and posteriorly curved in complete arcade. Crocodylians retain the basic diapsid snakes. When the teeth attach to the bone by sitting in architecture, although the upper or superior temporal sockets as in crocodylians, they are referred to as theco-fenestra is small (Fig. 2.18). In lepidosaurs, only Sphen-dont (Fig. 2.19). Pleurodont teeth found in most lepido-odon retains the two fenestrae. Squamates have only one saurs arise from a one-sided groove in the jaw. Acrodont upper fenestra or none at all. In squamates with only one teeth, which attach directly to the bone surface, occur in upper fenestra, the lower temporal arch (composed of two lizard clades. Tooth replacement is continuous the squamosal, quadratojugal, and jugal) has been lost.

throughout life, except in most acrodont forms, in which In squamates with no fenestrae, the upper arch (composed teeth are replaced in juveniles.

of the squamosal and parietal) or the upper and middle The skulls of turtles and all other extant reptiles are arches (composed of the squamosal and postorbital) have distinct (Fig. 2.18). In the turtle skull, the bony temporal been lost.

Sq

Po

Po

Po

METAKINESIS

STREPTOSTYLY

Sq

Neuro—

Dermatocranium

Quadrate

cranium

Modified diapsid

Modified diapsid

Modified diapsid

turtle

snake

lizard

Spenodon

All squamates

Mammals

PROKINESIS

MESOKINESIS

P Po

Po

Sq

P Po

Sq

Sq

Diapsid

Synapsid

Euryapsid

Squamate snake

Scleroglossan lizard

Po

Orbit

P

FIGURE 2.21 Evolution of jaw structure and function in squamates.

Sq

Clockwise from upper left, ancestors of squamates had rigid jaws and skulls such that the skull lifted as a unit when opening the mouth (meta-Qj J

kinesis). The “hanging jaw” of squamates (streptostyly) allowed rotation Anapsid of the lower jaws on the quadrate bone. Scleroglossans have kinetic joints FIGURE 2.20 Evolution of skull openings (fenestre) in modern rep-in the skull located behind the eyes (mesokinesis), and snakes have an tiles. Variation exists in the openings (fenestre) behind the orbit and the extra joint located anterior to the eyes (prokinesis). Increased flexibility position of the postorbital (Po) and squamosal (Sq) bones that form the of the skull allows greater prey-handling ability. The red circle with a arch from the orbit to the back of the skull. The anapsid (closed) condi-cross indicates focal point of rotation.

tion is thought to be ancestral. Lizards (including snakes) clearly have modified diapsid (two fenestre) skulls. Turtles, which have been placed feeding and defense behaviors. The jaw’s depressor and historically in the Parareptilia based on the absence of a second fenestra, adductor muscles arise from within the temporal arcade more likely have a highly modified diapsid skull in which both fenestre and attach to the inside and outside of the mandible.

have closed. Other bones shown include the quadratojugal and the jugal.

In highly kinetic skulls, muscles are more finely subdi-Adapted from Kardong, 2006.

vided and permit a wider range of movements of the individual bones, including those of the upper jaw. Throat The loss of arches and fenestrae in the diapsid skull is muscles are typically flat sheets of muscles that extend associated with increased flexibility of the skull. Hinges onto the neck. Beneath these muscles, the hyoid muscles between various sections of the skull allow the skull to are thicker sheets and longer bundles that attach the hyoid flex, a process known as kinesis (Fig. 2.21). A hinge can plate and processes to the mandible and to the rear of the occur in the back of the skull (a metakinetic joint) between skull and the cervical vertebrae.

the dermal skull and the braincase at the parietal–supraocciptal junction; this hinge is the oldest kinetic joint and occurred early in reptilian evolution and today occurs in VERTEBRAL COLUMN

Sphenodon. Two other joints developed in the dermal roofing bones. A dorsal mesokinetic joint lies between The amphibian vertebral column combines rigidity and the frontals and parietals in many lizards, and in many strength to support the head, limb girdles, and viscera, snakes, a prokinetic joint occurs at the contact between and yet it allows enough flexibility to permit lateral and the nasals and the prefrontals or frontals. The most dorsoventral flexure of the column. These seemingly striking kinesis of the lepidosaurs, particularly in snakes, conflicting roles are facilitated by the presence of sliding is streptostyly or quadrate rotation; each quadrate is and rotating articular facets on the ends of each vertebra loosely attached to the dermocranium and has a free ven-and by overlapping sets of muscular slips linking adjacent tral end. This loose ligamentous attachment allows the vertebrae.

quadrates to rotate and to swing forward and backward, Each vertebra consists of a ventral cylinder, the cen-and inward and outward. Streptostyly enhances the jaw’s trum, and a dorsal neural arch that may have a dorsal pro-grasping ability and increases the gape.

jection, the neural spine (Fig. 2.22). The anterior end of The complexity in the arrangement and subdivision of the centrum articulates with the posterior end of the pre-muscles mirrors the diversity of the bony architecture of ceding centrum. These central articular surfaces are vari-the head. Reptiles lack facial muscles, but the diversity ously shaped. In opisthocoelous vertebrae, the anterior of jaw and tongue muscles permits a wide range of surface is convex and the posterior surface is concave.

Salamandra salamandra Crocodylus acutus such as reptiles and mammals, and do not extend more than halfway down the sides.

The first postcranial vertebra, the atlas, is modified to create a mobile attachment between the skull and the transverse process

vertebral column. The atlantal condyles on the anterior surface articulate with the paired occipital condyles of the skull. The succeeding vertebrae of the trunk match the general pattern previously described. The number centrum

and shape of the vertebrae differ in the three amphibian groups. Salamanders have 10 to 60 presacral vertebrae, centrum

including a single atlas or cervical vertebra and a variable number of trunk including a single atlas or cervical vertebra and a variable number of trunk vertebrae. The trunk vertebrae are all neural arch

prezygo—

similar and have well-developed zygapophyses, neural postzygopophysis

pophysis

spines, and usually bicapitate, or two-headed ribs. Rather prezygo—

postzygo-

than exiting intervertebrally between neural arches of adja-pophysis pophysis

cent vertebrae as in other vertebrates, the spinal nerves of salamanders often exit through foramina in the neural arches. Postsacral vertebrae are always present in variable para—

transverse process

pophysis

numbers and are differentiated into two to four precaudal (cloacal) and numerous caudal vertebrae. Caecilians have 60 to 285 vertebrae, including a single atlas, numerous trunk vertebrae, no sacral vertebrae, and a few irregular Early tetrapod

bony nodules representing precaudal vertebrae. The trunk postzygo—

prezygo-

vertebrae are robust with large centra and neural spines; pophysis tuberculum

neural

pophysis

most bear bicapitate ribs. Frogs have 5 to 8 presacral verteb-arch rae. The atlas (presacral I) lacks transverse processes, which diapo—

are usually present on all other presacral vertebrae. Ribs are physis

absent in most frogs but are present on presacrals II through IV only in Ascaphus, Leiopelma, discoglossids, bombinator-ids, and pipids. Each sacral vertebra has large transverse processes called sacral diapophyses, although whether they rib

are true diapophyses is uncertain. The sacral vertebra articu-centrum lates posteriorly with an elongate urostyle, which represents a rod of fused postsacral vertebrae (Fig. 2.23).

capitulum

parapophysis

intercentrum

The musculature of the vertebral column consists of epaxial (dorsal trunk) muscles and hypaxial (flank or ventral trunk) muscles. The epaxial muscles consist largely of longitudinal slips that link various combinations of adja-FIGURE 2.22 Anterior and lateral views of vertebral morphology of cent vertebrae. These muscles lie principally above rib the tetrapods Salamandra salamandra and Crocodylus acutus and a sche-attachments (apophyses) and attach to the neural arches matic lateral view of an early tetrapod. Adapted in part from Francis (1934), Mook (1921), and Goodrich (1930).

and spines. These muscular components provide rigidity and strength to the vertebral column. The hypaxial mus-In procoelous vertebrae, the anterior surface is concave cles support the viscera and contain the oblique muscle and the posterior surface is convex; in amphicoelous ver-series that occurs on the flanks and the rectus muscle tebrae, both surfaces are concave. Intervertebral discs, series that occurs midventrally along the abdomen.

usually of fibrocartilage, lie between central surfaces of The trend for increased rigidity of the vertebral column adjacent vertebrae. A pair of flat processes extends from that began in early tetrapods is further elaborated in reptiles.

the prezygapophyses and postzygapophyses that form the The vertebrae form a firmly linked series and additionally anterior and posterior edges of the neural arch, respec-elaborated intervertebral articular surfaces interwoven with tively (Fig. 2.22). These processes form another set of a complex fragmentation of the intervertebral muscles.

articulations between adjacent vertebrae. Articular sur-In reptiles, vertebral rigidity is augmented by regional dif-faces for the ribs lie on the sides of each vertebra; a diapo-ferentiation of the vertebrae. This regionalization permits physis lies dorsal to the base of the neural arch and a different segments of the column to have different directions parapophysis lies on the side of the centrum. Ribs are and degrees of movement and is reflected in the architecture much shorter in amphibians than in the other tetrapods, of both bones and muscles.

Hyla versicolor Cryptobranchus alleganiensis phalanges procoracoid

phalanges

radius

metacarpals

metacarpals

carpals

carpals

clavicle

ulna

coracoid

radioulna

humerus

scapula

sternum

coracoid

humerus

sternum

transverse

sacral dia—

transverse

astragulus

process

pophysis

process

femur

ilium

phalanges

urostyle

metatarsals

pubis

tarsals

phalanges

epipubis

metatarsals

calcaneum

tibiofibula

ischium

tibia

tarsals

pubis

fibula

ischium

ilium

femur

FIGURE 2.23 Postcranial skeletons (ventral view) of a gray treefrog (Hyla versicolor) and a hellbender (Cryptobranchus alleganiensis). Adapted from Cope (1898).

Reptilian vertebrae and vertebral columns are variable these articular surfaces determines the amount of lateral across taxa, but some features are shared by most reptiles flexibility. When the articular surfaces are angled toward (Fig. 2.22). The centra are the weight-bearing units of the the horizontal plane, flexibility between adjacent vertebrae vertebral column. Each centrum is typically a solid spool-increases, but if the surfaces are angled toward the vertical shaped bone, but in Sphenodon and some geckos, the plane, rigidity increases. The pedicels also bear the articu-notochord persists and perforates each centrum. A neural lar surfaces for the ribs. For two-headed ribs, the upper sur-arch sits astride the spinal cord on each centrum. The legs face is the transverse process or diapophysis, and the lower or pedicels of each arch fuse to the centrum or insert into surface is the parapophysis. The ribs of extant reptiles are notches on the centrum. Neural spines vary from short to single-headed and articulate with the transverse process in long, and wide to narrow, depending upon the position all lineages except crocodylians. In many lepidosaurs, within the column and the type of reptile. The interverte-accessory articular surfaces occur at the base of the neural bral articular surfaces, or zygapophyses, consist of an spine; a zygosphene projects from the front of the arch into anterior and a posterior pair on each vertebra and arise a pocket, the zygantrum, on the rear of the preceding verte-from the top of pedicels. The articular surfaces of the ante-bra. The articular surfaces between the centra are variable, rior zygapophyses flare outward and upward, and the pos-but the procoelous ball-and-socket condition is widespread, terior surfaces are inward and downward. The angle of occurring in all extant crocodylians and most lepidosaurs.

Sacrals

Lumbars

Thoracic vertebrae

Cervicals

Caudals

Cervical ribs

Interclavicle

SternumProcoracoid

Gastralia

Thoracic ribs

FIGURE 2.24 Partial skeleton of a crocodylian showing the variation in structure of vertebrae. The vertebral column is divided into five regions. Note the location of the gastralia (floating “ribs”). Redrawn from Kardong, 2006.

The most variable central articular patterns occur in the cer-lengths of different turtle species arise from the elongation vical vertebrae, where, for example, procoelous, opistho-or shortening of vertebrae. Of 10 trunk or dorsal vertebrae, coelous, and biconvex centra exist in the neck of an the first and last are attached but not fused to the carapace.

tion of energy for reproduction and results in lower reproductive output. Sceloporus merriami is a sit-and-wait of the breeding season, males defend the entire home predator. In contrast, lizards that actively search for prey range; during this time, the home range and territory would be expected to have large home ranges. Actively are the same.

foraging lizards, such as Aspidoscelis and Cnemidophorus, In most species, home range size generally decreases have relatively large home ranges throughout which they as food availability or density increases (Fig. 8.3). In at search for prey.

and tend to move at night. When streams dry during droughts or seasonally, the turtles often aestivate under-ground in terrestrial habitats, and they are able to with-300

stand water deprivation for extended time periods.

A long-term capture–recapture study on these turtles revealed that males move farther than females and that 200

adults in general move farther than juveniles. Although average distance that males and juveniles moved was not associated with body size, distance moved varied with body size in females, but in a curvilinear manner. The Area in square meters 100

largest (and presumably oldest) females moved less than did moderate-sized adult females but considerably more than small adult females (Fig. 8.5). Movements of these turtles occur within pools, between pools in a particular 82 83 84

all 82 83 84

all 82 83 84

all 82 83 84

all 82 83 84

all 82 83 84

all

complex of pools within a stream, between complexes, males

females

males

females

males

females

Grapevine Hills

Boquillas

Maple Canyon

and even between drainages, although the latter is a rare event. A vast majority of Sonoran mud turtle activity FIGURE 8.4 Home range size in Sceloporus merriami varies between occurs within a single pool or its associated pool complex.

sexes, among years, and among three different sites in the Chisos Mountains of west Texas. Boquillas, the site with the most extreme (hot and Because most mud turtle species live in streams, home dry) environment, imposes thermal constraints on lizard activity, resulting range length serves as a good metric for comparisons in small home ranges. Adapted from Ruby and Dunham, 1987.

among species. Among the few mud turtles for which data exist, Sonoran mud turtles have the longest home ranges The Australian elapid, Hoplocephalus bungaroides, (298 m for adult males, 104 m for adult females). On centers its home range around retreat sites in rocky outcrops average, Sonoran mud turtles also move greater distances and tree hollows and remains inactive most of the time.

than most other mud turtles, but not K. flavescens. Both Male home ranges of H. bungaroides overlap very little K. sonoriense and K. flavescens live in habitats that during the breeding season, but home ranges of females experience seasonal drying, and as a result, their relatively are often within the home ranges of males. Females carrying long-distance movement patterns may be associated eggs move less than do nonreproductive females or males with finding water. Similar to many aquatic amphibians and as a result have smaller home ranges. Home range and reptiles, not only is the specific aquatic habitat of size in males and females varies among years, apparently mud turtles critical to sustain natural and females varies among years, apparently mud turtles critical to sustain natural populations, but in response to the relative abundance of their mammalian associated terrestrial habitats and access to other aquatic prey.

habitats are as well.

Aquatic environments offer special challenges in terms of space use for amphibians and reptiles, not only because of their three-dimensional nature, but also 6

because they fluctuate depending on rainfall or drought.

Adult

Aquatic snakes and turtles often have relatively large males

5

home ranges, and their home ranges can change seasonally. During particularly dry years, their entire area of 4

activity can shift if a pond or stream dries. Most leave ed [m] ± SE)

their home ranges for brief periods to deposit eggs.

v

3

Surprisingly, one of the larger aquatic (marine) turtles, Adult

Juveniles

Chelonia mydas, has one of the smallest home ranges females

2

once they settle in an area to feed. These turtles create a submarine pasture and focus their grazing in that small Ln (distance mo

area. In contrast, another sea turtle, Dermochelys coria-1

ceae, appears to move constantly, tracking the seasonal blooms of its jellyfish prey.

0

The Sonoran mud turtle (Kinosternon sonoriense) lives 55

65

75

85

95

105

115

125

135

145

Carapace length (mm)

in rivers, streams, and man-made impoundments in the Sonoran Desert of Arizona and northern Mexico and, even FIGURE 8.5 Adult Sonoran mud turtles move more than juveniles, and for adult males and juveniles, distance moved does not increase much though abundant in many areas, is often missed by people with turtle size. However, in adult females, small and very large females observing wildlife. These turtles spend much of their time move less than females of moderate size. Note that the y-axis is natural-under rocks or other objects under water in their habitats log transformed. Adapted from Hall and Seidl, 2007.

A few other patterns of space use occur in ambush-for-greatest abundance of their preferred prey. The bushmas-aging species that do not fit the typical home range model ter, Lachesis muta, moves to microhabitats where prey because of regular long-distance shifts in primary foraging capture is likely, such as along the edge of a fallen log sites. Individual prairie rattlesnakes, Crotalus viridis, wan-or along trails. The snake typically remains in one spot der until they locate an area of high prey density. They for several weeks, rarely changing position except to raise remain in that area until prey density reaches some lower the head at night while “searching” for passing prey. After threshold and prey capture becomes infrequent, after a meal, the snake remains at the site 2–4 more weeks which they move to a new site. Likewise, water snakes, digesting the prey and then seeks out a new foraging site.

Nerodia sipedon, appear not to have traditional home It remains a mystery whether some sort of large, circum-ranges. Because home range size continues to increase scribed area is involved or whether bushmasters simply with the number of times an individual is captured, use move along a nonrepeating track.

of space appears to consist of a series of activity centers The most obvious examples of age-specific differences that shift spatially. Similar use of space has been observed in space use can be found in species with complex life in other snakes.

cycles. Many larval amphibians live in aquatic environ-Water pythons, Liasis fuscus, migrate seasonally to fol-ments and the adults live in terrestrial environments, so low their prey, dusky rats (Rattus colletti), which shift little overlap in larval and adult use of space is expected.

their dry season distribution from soil crevices in the back-Adults of many amphibians with complex life histories swamp areas in the Northern Territory, Australia, to levee have home ranges, but whether larvae have home ranges banks up to 12 km away during the wet season when the is unclear. In arboreal lizards, juveniles use different floodplain is inundated (Fig. 8.6). At the end of the wet perches than adults or disperse in response to population season, the snakes return to the floodplain, even though density. Hatchlings of the Neotropical lizard Anolis rat density remains high on the levee. Adult male rats, aeneus prefer perches averaging 1.35 cm in diameter, which reach a larger size than females, are more abundant whereas adult females and males prefer much larger and reach larger size on the floodplain due to higher levels perches (8.5

larger and reach larger size on the floodplain due to higher levels perches (8.5 and 38.6 cm diameter, respectively). Hatch-of moisture and nutrients, and these are preferred. The ling perches are closer to the ground (14.4 cm on average) snakes shift their seasonal activity to coincide with than those of adult females and males (50.6 and 169.7 cm, respectively). Home range size is also much smaller for hatchlings. Because of ontogenetic differences in perch characteristics, hatchlings occupy different microhabitats than adults.

N

Nevertheless, some examples of age-related variation in home range size exist in reptiles, and as more studies are done, additional examples will be documented.

Females of Australian sleepy lizards, Tiliqua rugosa, give birth within their home ranges. During spring of their first Backswamp

Floodplain

year of life, juveniles maintain home ranges that overlap much more with the home range of their mother than with home ranges of adjacent adults, even though no parental care occurs. Juvenile home ranges are about 60% of the size of home ranges of females, and juveniles move less er

often and for shorter distances than adult males or females. Adult males have home ranges that average about Fogg

20% larger than those of adult females.

Dam

Harrison

Adelaide Riv

Gopher tortoises (Gopherus polyphemus) were once Woodland

Dam

abundant animals across the Coastal Plain of the southern 1 km

United States. Harvesting of these animals for food during FIGURE 8.6 Locations and movements of water pythons (Liasis fus-the last 2 centuries and, more recently, rapid loss of habi-cus) in the Northern Territory of Australia. Solid circles indicate posi-tat, have resulted in drastically reduced numbers of these tions of snakes during dry season when the floodplain is dry and the backswamp contains deep crevices; open circles indicate positions of large tortoises. Much of the time, these conspicuous ani-snakes during wet season when the floodplain is wet and the backswamp mals remain inside deep burrows in sandy soils, making crevices are closed. Snakes move to high ground in wet season because relatively short forays to forage, find mates, and occasion-rats become rare in low areas. Snakes move to the backswamp and dam ally construct new burrows. Home ranges of adult, sub-during dry season because rats there are larger. Arrows show movement adult, and juvenile gopher tortoises vary considerably, patterns for two radio-tracked individuals (one male and one female) showing that individuals move long distances. Adapted from Madsen depending on sex, duration of study, and the number of and Shine, 1996.

movements made by individual tortoises. Home ranges

vary from as small as 0.002 hectares to as large as 5.3

Imagine two individual males in a population, one that hectares, with most in the range of about 0.01–2.5

defends good places to forage from other males but allows hectares. Using a combination of techniques (thread-females into those areas and breeds with them. The other spools, transmitters, and permanent marks), David Pike male controls no resources and as a consequence does not studied the home range and movements of hatchlings on attract females. However, he can easily find enough food the Atlantic Coast of central Florida. Dispersal from the to keep himself healthy by moving around. The territorial nests was random with respect to direction. Hatchlings male, as the result of his territory defense behavior, might, moved considerably following hatching (late summer), hypothetically, be more vulnerable to predation. Neverthe-very little during their first winter—a time period in which less, he has many more opportunities for mating than the yolk reserves provide most hatchling nourishment—and other male. He actually may not live very long, but long then resumed movements the following spring and sum-enough to reproduce, so that when predators kill him, he mer. Burrow construction followed a similar pattern. Even will have left offspring. In the meantime, the nonterritorial though the number of moves was high following hatching, male remains healthy and lives a long life. Representation distance moved was low and remained low until the of his genes ends in that generation, whereas territorial following spring and early summer. Home range size genes (even with the risk attached) are passed on to the (minimum convex polygon) of (even with the risk attached) are passed on to the (minimum convex polygon) of hatchling tortoises that next generation. Alternatively, the long-lived, healthy male were radio-tracked varied from 0.014–4.81 hectares could replace a territorial male that was eliminated, shift (average 1.95 Æ 2.12 hectares). The considerable dis-his behavior to territorial, and achieve a high reproductive tances that hatchlings disperse, especially after their yolk success. In this scenario, both types of male reproductive is depleted, likely allows hatchlings to develop a spatial strategies are maintained in the population.

map of their environment and has the added benefit of Of course, social systems and the evolution of social moving individuals away from the nest site, spreading systems are not this simple—for example, a nonterritorial them out and possibly reducing predation. By the time male might be able to sneak a few matings with females liv-each hatchling cohort reaches sexual maturity, dispersion ing within the home range of territorial males. Thus, non-of individuals would also reduce inbreeding. A key ele-territorial genes can be passed on but at a lower frequency ment of this study is that it brings movement patterns of than territorial ones. Territoriality generally is linked with hatchlings into an overall view of the ecology of gopher mate choice and other aspects of social systems (see Chap-tortoises. As we have seen with many other animal species ter 9).

impacted by human activities (e.g., sea turtles), under-Given the preceding, a territory can be defined explic-standing ecology of hatchlings is critical to developing itly as any defended area that meets the following three species-management strategies.

conditions: It is a fixed area, it is defended with behavioral acts that cause escape or avoidance by intruders, and these Territories

behavioral acts result in exclusive use of the area by the resident territory holder.

A territory is the area within a home range that is actively Territoriality is well known in some frogs and sala-defended against intruders, usually because the area manders but unknown in caecilians. Because caecilians includes a defendable resource or has some other quality are extremely cryptozoic, territoriality may exist but be that is better than adjacent areas. Defense results in exclu-undocumented. The observations that sexual dimorphism sive use of the territory by the resident. In amphibians and exists in head size and is not related to sexual differences reptiles, when territoriality occurs, males are most often in prey, and the existence of bite marks on some indi-territorial and females are not. In a few species, females viduals suggest that territoriality could occur in some defend a territory as well. Most often, territories defended caecilians. In frogs, acoustic signals serve as avoidance by males contain females whose home ranges are included displays, and outright aggression can occur in threat within the male territory. Because territoriality allows displays. Territoriality occurs most often in frogs with an individual to maintain control over resources, it extended breeding seasons and is rare or does not occur involves competition among individuals within species in explosive breeders or species with very restricted for resources that ultimately contribute to individual fit-breeding seasons. It also occurs in frogs with extended ness. Natural selection favors those individuals that con-parental care (e.g., dendrobatid frogs). In bullfrogs, males trol and use resources in a way that positively influences establish territories that contain good oviposition sites, their reproductive success. Discovering the connection which they defend with threats, displays, or wrestling between resource control and reproductive success is matches. Large males win a majority of contests with seldom easy. Every aspect of territorial behavior has other males, indicating that male size determines domi-costs, and obviously, the gains associated with territorial-nance. Good oviposition sites have high embryo survival.

ity must outweigh the costs if territorial behavior is to be The two primary sources of mortality, developmental maintained through time.

abnormalities and leech predation, are reduced at sites

with cooler temperatures (< 32C) and the appropriate interactions between males are rare, even though males vegetation structure to reduce leech predation on the eggs frequently perform push-up displays. Males remain in and embryos. Females are attracted to territories with a the same territories year after year. Most likely, males potential for low egg mortality, and because large males establish territories early in life, remain in those territories, control these territories, they mate with more females.

and use social signals to remind neighbors that they still In this situation, the resource base for territories is high-inhabit the territory. Because aggression is energetically quality egg deposition sites, and the payoff is increased expensive and potentially risky, it may not occur in reproductive success for defenders of these sites. Sneak S. occidentalis, or at least it may occur only rarely. This or satellite males that are not territory holders occasionally example shows that definitions of home range and terri-intercept females and mate with them.

tory are often not as clear as we might like. Not only are Most data on salamander territoriality is based on stud-territories of S. occidentalis not defended aggressively ies of a single clade, Plethodon, which is composed and regularly, but males allow at least one other male to largely of terrestrial species. Plethodon cinereus marks overlap in some part of their territory. Descriptors like territories with chemicals (pheromones). In the laboratory, home range and territory are conceptually useful, but it adult male and female P. cinereus show "dear enemy" recis important to keep in mind that they are just descriptors, ognition, in which they are less aggressive toward recog-and detailed observations frequently reveal that patterns nized enemies than they are toward unfamiliar intruders.

of space use are intrinsically more complicated.

Evolutionarily, this reduces energy spent in continual high-level encounters with close neighbors that are unlikely to go away but will maintain distance if reminded Evolution of Territoriality

that a territorial holder is in place. Combat, often directed at the tail, can occur, and tails can be lost as a result of Studies conducted on use of space by individuals within encounters. Tails are important energy stores for reproduc-and between species reveal considerable variation in the tion; consequently, the loss of a tail negatively affects proportions of home ranges that are defended. Some spe-reproductive success. Bites during combat are also cies defend the entire home range, others defend specific directed at the nasolabial grooves, which are important sites within the home range, and others do not appear to transmitters of chemical signals.

defend any part of the home range. Males of many species The Central American dendrobatid frog Oophaga without territories aggressively attack other males that pumilio lives in leaf litter on the forest floor. Males main-approach females either within the male's home range or tain territories that they aggressively defend from other while the resident is courting the female (see Chapter 9).

males. Males call from tree bases or fallen logs, and the Although adaptive scenarios can be devised to explain distribution of these structures determines inter-male dis-territorial defense in nearly every amphibian or reptile, tance to a large extent. Many males remain in restricted similarities in behavior among closely related species areas over long time periods and, when displaced experi-often reflect common ancestry; individuals of many mentally, return to their territories. Females deposit eggs species behave the way their ancestors did.

in terrestrial oviposition sites, and males use elevated A close examination of defense behavior in lizards sug-perches for calling; the location of male territories must gests that evolutionary history determines a large part of include resources.

behavioral patterns. Among studied lizards, defense is Food available to individual animals varies both tem-accomplished by direct combat, threats, or simple avoid-porally and spatially and can influence space use. Males ance. Combat involves biting, wrestling, or any behaviors and females of the montane lizard Sceloporus jarrovi involving physical contact between two individuals. Threat defend territories against conspecifics of the same size or refers to aggressive communication in which no physical sex. Territories that contain relatively more food tend to contact is made. Threats most often involve push-up dis-be smaller than territories with less food, independent of plays, throat expansion, or high-intensity erection and con-the differences in territory size associated with lizard body traction of the dewlap. Avoidance defense is based on size. Adding food to the territory of S. jarrovi results in a indirect displays such as chemical signals. Push-up dis-shift in space use; the site where food is added becomes plays are presented from a distance where the primary goal the center of the territory. In this instance, food availabilis to assert presence. Other examples of avoidance displays ity appears to determine the location of the territory. In the exist as well. The size of the area defended can range from Western fence lizard, Sceloporus occidentalis, home all or part of the home range to none of it (Table 8.2). An ranges of males overlap considerably, from 28–67% of examination of the distribution of home range defense on space being used by at least one additional male and a lizard phylogeny shows that major shifts have occurred often several males. However, territory overlap is much during the evolutionary history of lizards in the proportion smaller, ranging from 14–52%, and in most cases, overlap of the home range defended (Fig. 8.7). This phylogenetic occurs with only a single male. Nevertheless, aggressive analysis shows that territoriality (defense of all or part of

TABLE 8.2 Ten Behavioral Categories for Lizards Based on Aggressive Defense of Resources.

Defense area

Defense style

All or part of home range

Specific site (Basking, Shelter)

No area (Self)

Combat

Type I

Type IV

Type VII

Threat

Type II

Type V

Type VIII

Avoidance

Type III

Type VI

Type IX

Type X - Affiliative aggregations or random distribution of animals Note: Each category is defined by the intersection of defense style and defense areas.

Source: Adapted from Martins, 1994.

Other Patterns of Space Use

Many amphibians and reptiles brood or guard nests, and remain near the eggs until the eggs hatch (Fig. 8.8). The space the brooding parent uses is much smaller than the home range and is not necessarily within the home range Crotaphytinae

Iguaninae

Phrynosomatinae

Polychrotidnae

Tropidurinae

Chamaeleonidae

Gekkonidae

Xantusiidae

Lacertidae

Teiidae

Scincidae

Cordylidae

Anguidae

Varanidae

used during the nonbrooding season. Females of the four-toed salamander, Hemidactylium scutatum, brood eggs in Lacertiformes

clumps of peat moss along slow-moving streams, remain-Anguimorpha ing restricted to the nest for an extended time period. Lung-Iguania less salamanders in the genus Plethodon brood egg clutches in moist areas under rocks and inside of rotting logs (Fig. 5.22). Female broad-headed skinks, Plestiodon Autarchoglossa

laticeps, brood clutches of eggs in partially decomposed pockets within hardwood logs, rarely leaving until after the eggs hatch, and other Plestiodon species brood their eggs in a variety of relatively sealed chambers inside of FIGURE 8.7 Phylogeny for lizards showing the evolutionary distribu-logs, under surface objects, or in the ground (Fig. 5.16).

tion of home range defense. The ancestor of all lizards presumably Aggregations occur in a wide variety of amphibians and defended the entire home range with an overall reduction in area reptiles for a number of reasons (Table 8.3). All aggrega-defended as lizards diversified, and this behavior is carried through in tions represent nonrandom use of space, and most often clades indicated by black. Site defense (clades in red) evolved in the are centered on scarce resources. For amphibians, the most ancestor to Autarchoglossans. A lack of home range or site defense evolved independently twice, in the ancestor to the Lacertiformes and obvious examples are aggregations of adults in ponds or in the ancestor to Anguimorpha. Taxonomy has been revised for consis-other bodies of water during breeding events. Spadefoots tency, but relationships to behavioral traits remain unchanged. Adapted arrive by the thousands to breed in temporary ponds, as do from Martins, 1994.

many other explosive-breeding frogs. Large numbers of Physalaemus (Leiuperidae) enter ponds that form during the home range) is ancestral to all lizards and that adaptive the early wet season in seasonally wet open areas in South scenarios are not necessary to explain territoriality in the America, yet locating a single individual during the dry Iguania and Gekkonidae. The loss of territoriality within season is difficult.

the scleroglossans (particularly the Teiidae, Lacertidae, Tadpoles of a variety of anuran species form dense Anguidae, and Varanidae) most likely reflect the conse-

“schools” that move about in ponds, presumably to offset quences of a switch from a sit-and-wait foraging mode to predation. In some, such as Hypsiboas geographicus (Hylian active-or wide-foraging mode (see Chapter 10). We dae), Leptodactylus ocellatus (Leptodactylidae), and Litho-point out that these conclusions rest on the assumption that bates heckscheri (Ranidae) not only are the schools huge, the phylogeny on which this analysis was done reflects the but the tadpoles are large as well, often exceeding 60 mm evolutionary history of squamate reptiles. If recent nuclear-in total length. Consequently, the schools appear as huge gene-based relationships of squamate higher taxa prove to dark masses in the ponds where they occur. Schooling better reflect evolutionary history, then the sequence of behavior has evolved independently many times in anurans.

events leading to territoriality among lizard clades will A variety of species of salamanders, including Plethodon need to be reconsidered (see Chapter 20).

glutinosus, Ambystoma macrodactylum, and Ambystoma

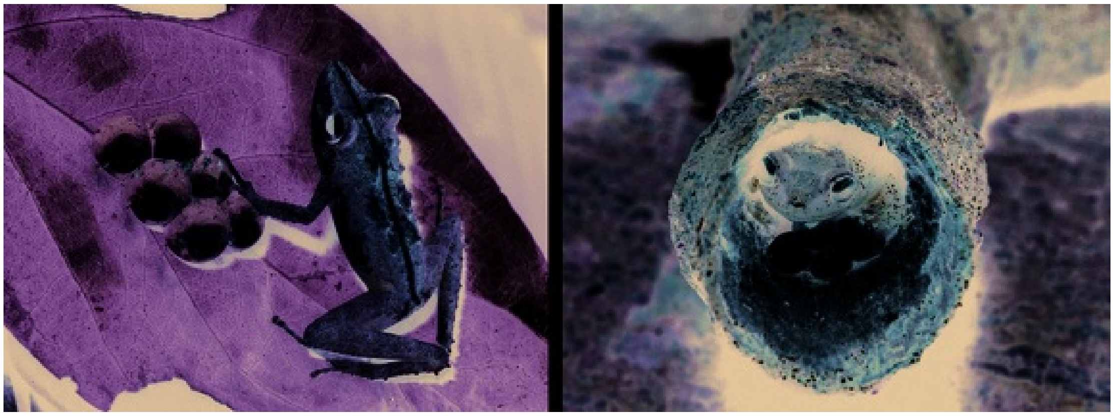


FIGURE 8.8 Amphibians and reptiles usually remain in one place while brooding or attending eggs. The ceratobatrachid frog Platymantis (undescribed species) broods its eggs on leaves, whereas the microhylid frog Oreophryne (undescribed species) broods its eggs inside of hollows in branches. Photographs by Stephen J. Richards.

TABLE 8.3 Examples of Social, Nonreproductive Aggregations of Amphibians and Reptiles.

Taxon	Purpose
Salamanders, mixed, seven species	Hibernation
Plethodon glutinosus	Estivation
Salamandra salamandra	Hibernation
Rhinella tadpoles	Schooling
Hyla meridionalis, Pelodytes, Triturus, Podarcis	Hibernation
Limnodynastes juveniles	Water conservation
Xenopus laevis tadpoles	

Xenopus laevis tadpoles

Schooling

Terrapene ornata

Hibernation

Terrapene ornata and Kinosternon flavescens Hibernation

Crocodylian hatchlings

Reduce predation

Alligator mississippiensis

Feeding

Amblyrhynchus cristatus

Sleeping

Diadophis punctatus

Water conservation (?)

Pelamis platurus

Feeding

Storeria dekayi

Water conservation (?) and hibernation Thamnophis (three species), three other snake genera, Hibernation

Ambystoma, and Pseudacris

Coleonyx variegatus

Water conservation

Typhlops richardi

Water conservation (?)

Sources: Amphibians—S, Bell, 1955; Pg, Humphries, 1956; Ss, Lescure, 1968; R., Wassersug, 1973; Hm, Van den Elzen, 1975; L, Johnson, 1969; Xi, Wassersug, 1973;.

Reptiles—To, Carpenter, 1957; C and Am, Lang, 1989; Ac, Boersma, 1982; Dp, Dundee and Miller, 1968; Pp, Kropach, 1971; Sd, Noble and Clausen, 1936; T, Carpenter, 1953; Cv, Lancaster et al., 2006; Tr, Thomas, 1965

T, Carpenter, 1953; Cv, Lancaster et al., 2006; Tt, Thomas, 1965.

tigrinum, aggregate in damp retreats when the terrestrial as well as functioning in social behavior. Chemical cues environment becomes excessively dry. In the proteiid also appear to attract other individuals, resulting in sev- salamander, Proteus anguinus, individuals aggregate in eral individuals sharing shelters. Garter snakes aggregate shelters in the caves in which they live, usually under in large numbers for both overwintering and mating, and stones or in crevices. Experiments show that homing in rattlesnakes aggregate in large numbers in high latitudes on a retreat is accomplished by use of chemical cues, and at high elevations to overwinter in dens. In fall, which provide directional information to the salamanders the lizard Sceloporus jarrovi aggregates along crevices

escape predators. Most of these movements take place within the individual's home range. The benefits of moving are offset by the costs of moving (usually energy or risk of mortality). For species with cryptic morphology or coloration, moving upsets crypsis and can accrue a survival cost. Active or wide-foraging species tend to move considerably more and expend more energy, doing so within their home ranges, than do species that use the sit-and-wait foraging mode. Their alert behavior and rapid response to predators offset the cost of exposure.

Both extrinsic and intrinsic factors influence movements of amphibians and reptiles (Table 8.4). Herpetolo-gists rapidly learn to take advantage of environmentally induced patterns of movements; amphibians, in particular, can be collected or observed in great numbers on rainy nights during spring in temperate zones and on the first rainy nights during tropical wet seasons. Rattlesnakes (particularly Crotalus viridis and C. oreganus) occur in large numbers when they aggregate for overwintering.

Long-term studies on slider turtles have identified factors that cause movements in turtles (Table 8.5). These factors likely apply to most species of amphibians and reptiles.

Movements outside the home range carry additional risks compared with movements within the home range, largely FIGURE 8.9 A basking aggregation of marine iguanas, Amblyrhynchus cristatus. (K. Miyata)

because traveling occurs in areas with which the individual has little or no familiarity. When these movements occur, they usually are related to breeding, finding food or in mountains of southeastern Arizona to overwinter.

water no longer available in the home range, or overwin-They frequently bask in sun along the crevices to gain tering, or such movements are in response to catastrophes heat, even though they are territorial during the activity (e.g., flooding).

season. Snakes and lizards aggregate at talus slopes in The most apparent dichotomy in movement patterns on northern Oregon because these areas are the best availa daily basis is diurnal versus nocturnal movement. Most able nesting sites. Fifty-one lizard eggs, 294 snake eggs, salamanders and frogs are nocturnal, but some species and 76 snakes were found in a patch of talus within an such as cricket frogs (Acris) and striped pond frogs area of 150 square feet. In tropical South America, (Pseudis limellum) are both diurnal and nocturnal.

aggregations of frogs can be found inside and under termite nests during the dry season. In addition to frogs, these aggregations often include snakes, lizards, and arthropods. The termite nests offer an environment where TABLE 8.4 Factors That Influence Movements temperature and humidity are moderated. These are but a of Individual Amphibians and Reptiles.

few examples of aggregations in amphibians and reptiles Environmental

Population

Individual

(Fig. 8.9).

Daily temperature

Density

Sex

patterns

Seasonal temperature

Sex ratio

Body size

MOVEMENTS, HOMING, AND MIGRATIONS

patterns

Humidity/rainfall

Age structure

Age

Most amphibians and reptiles move relatively little dur-Habitat type or Size structure

Physiological

ing their entire lifetime except when they are breeding.

condition

condition

Individual box turtles, Terrapene c. carolina, in Mary-Catastrophic events Disease/

Reproductive

parasitism

state

land, for example, moved very little over 30 years or Recent

more and remained in the same home range; similar experience

observations have been made on many other species.

Individuals move to forage or change foraging posi-Source: Adapted from Gibbons et al., 1990.

tions, pursue mates, defend territories, deposit eggs, or

TABLE 8.5 Causes and Consequences of Movements at the Intrapopulation and Interpopulation Level for Turtles.

Category

Purpose

Primary benefits gained by moving Intrapopulational

Feeding

Growth; lipid storage

(short-range)

Basking

Increased mobility due to body temperature increase; reduction of external parasites; enhanced digestion

Courtship and mating (adults only) Reproductive success

Hiding, dormancy

Escape from predators or environmental extremes Interpopulational

Seasonal

(long-range)

Seeking food resources

Growth; lipid storage

Nesting (adult females)

Direct increase in fitness

Mate seeking (adult males)

Direct increase in fitness

Migration (hibernation, aestivation) Survival

Travel from nest by juveniles

Initiation of growth

Departure from unsuitable habitat Survival

Adapted from Gibbons et al., 1990.

Movements of winter-breeding amphibians often occur season, caimans enter the flooded forest in search of during day and at night. The absence of daylight appears stranded prey. Among lizards, most are diurnal (e.g., all to trigger mass movements in Pseudacris crucifer, iguanians, teiids, gymnophthalmids), some are nocturnal P. ornata, P. nigrita, and Lithobates sphenocephala, and (e.g., many gekkonids), and some vary their diel activity, both temperature and moisture determine the specific at least on the surface, with season (e.g., helodermatids).

nights on which breeding will occur. On nights with low Among snakes, nearly every possible diel pattern of temperatures or no rainfall, breeding migrations do not activity occurs. Most desert snakes are nocturnal, but occur. The risk of movement during daytime for these some, like Masticophus flagellum, are strictly diurnal.

frogs may be tied to diurnal predators like birds. Dendro-Likewise, many tropical snakes are nocturnal, but some batid frogs are diurnal and sleep at night, often perched species, including all species of whipsnakes in the genus within 0.5 m of the ground on leaves of small plants.

Chironius, are diurnal (Fig. 8.10).

Brightly colored species (e.g., Dendrobates, Phyllobates) In the Mojave Desert of southern California, male side-offset predation by having noxious or poisonous skin winders (Crotalus cerastes) move an average of 185 m secretions and advertising their toxicity with aposematic each night while active, whereas nongravid females move coloration, whereas other species (e.g., the closely related only 122 m. Individuals are active on about 60% of the aromobatid frogs such as Allobates) offset diurnal preda-nights during their activity season. Greatest movements tion by cryptic coloration and behavior (see Chapter 11, of adult males occur during spring and fall mating sea-

“Chemical Defense”).

sons, which suggests that they are searching for females.

Depending on species, turtles can be diurnal or noctur-Activity ranges of individuals vary from 7.3–61 hectares; nal. Box turtles (Terrapene) and tortoises (Geochelone) males, females, and juveniles have similar activity are strictly diurnal, as are many aquatic turtles (e.g., ranges. Sidewinders appear to move randomly until fall, Apalone, Graptemys). Some species, like Chelydra ser-when their movements are directed toward overwintering pentina, appear to be active both during the day and at sites. Overwintering sites are usually located in rodent night. Crocodylians are active during both day and night, burrows at the interface between sand and alluvial habitat but much of their diurnal activity involves basking.

patches.

Caiman crocodilus in the Amazon of Brazil, for example, Freshwater turtles leave their aquatic habitats to dig basks on sandy banks of rivers and ponds during the day nests, search for mates, overwinter, or locate new aquatic and actively searches through its aquatic habitat for prey habitats when their original stream or pond dries up. Six at night. When water floods the forest during the wet turtle species, Trachemys scripta, Kinosternon subrubrum,

FIGURE 8.10 Some tropical colubrid snakes are diurnal, such as the tropical whipsnake, Chironius flavolineatus (left), but most are nocturnal, such as the burrowing snake Apostolepis bimaculata. (L. J. Vitt) Pseudemys floridana, Sternotherus odoratus, Chelydra 80

serpentina, and Deirochelys reticularia, are long-time males

residents of Ellenton Bay, a freshwater pond located approximately 2 miles residents of Ellenton Bay, a freshwater pond located approximately 2 miles from the Savannah River in South 60

Carolina. Adults of four other species, Pseudemys con-females cinna, Clemmys gutata, Chrysemys picta, and Kinosternon 40

bauri, occasionally enter Ellenton Bay. Juveniles of the latter four species have never been observed at the pond, and with the exception of P. concinna, a majority of non-Percent of sample 20

resident turtles were males (100% for K. bauri and C. picta, 80% for C. guttata). Only a single female P. con-0

cinna has entered the pond. Most of the nonresident turtles 0.2–1.0 1.1–2.0 2.1–3.0 3.1–4.0 4.1–5.0

?5.1

are males because long overland movements by males Distance between sites (km)

increases their probability of encountering females in FIGURE 8.11 Long-range movements based on straight-line dis-other aquatic habitats, whereas females have less to gain tances of Trachemys scripta between aquatic habitats in South Caro-by long-distance moves, particularly considering the lina. Travel between Ellenton Bay and Lost Lake were primarily over potential costs of increased risk of predation by terrestrial land. Exchanges in Par Pond could have been by a shorter overland predators. Overland ventures by T. scripta vary from 0.2

route or a longer route through water. Adapted from Gibbons et al.,

1990.

to 9 km, resulting in sightings of turtles in ponds other than their home ponds (Fig. 8.11). Many of the turtles return to their home ponds, indicating that these move-even though they may be buried in soil or leaf litter. A ments are not immigrations.

scintillation system detects radioactivity of the tags from In Malaysia, the semiaquatic snake Enhydris plumbae 2 meters away. The technique appears particularly suit-occurs in water buffalo wallows, slow-moving streams, able for particularly suit-occurs in water buffalo wallows, slow-moving streams, able for short-term studies, because the isotope has no rice paddies, and a variety of other aquatic habitats. Most apparent effect on salamander physical condition and individuals move very little, and 44% do not move at all the tags remain in place for about a month. This tech-

(Fig. 8.12). The snakes are active day and night but are nique is not useful for longer time periods because sala-observed on the surface at night. A partial explanation manders lose body weight, suffer skin lesions, and often for the low movement in E. plumbae is that many occur lose the tags after about 40 days. An early study using in small, isolated bodies of water (buffalo wallows), but the technique revealed that some salamanders are capa-even those in rice paddies move very little.

ble of orientation and subsequent homing when dis-Studying movement behavior of salamanders, espe-placed. Males of Plethodon jordani occupy home cially terrestrial species, is logistically difficult. By ranges that are about three times larger than those of inserting tiny tantalum-182 tags in the base of the tail females. Salamanders displaced between 22–60 meters of salamanders, individuals can be located in the habitat from their home ranges return to within 7 meters of their

25

throughout most of the Caribbean (Fig. 8.13). Their long Movements based on

journeys and ability to return to the beaches where they 20

trapping

were hatched suggest a complex navigational system.

15

10

5

Mass Movements

0

Mass movements occur in some amphibians and reptiles.

The use of terrestrial drift fences around amphibian breed-25

Movements based on

ing ponds has made it relatively easy to monitor the move-20

daily radiotelemetry

ments of amphibians, some of which are startling.

15

Ambystomatid salamanders and many frogs, especially 10

those that are explosive breeders, move en masse to and from breeding ponds. Metamorphs leaving breeding ponds 5

Number of records

often do so en masse as well. During a single year (1970), 0

2034 individuals of 14 species of frogs moved in or out of one permanent pond, and 3759 individuals of 13 species of 100

Movements based on

frogs moved in or out of another temporary pond in South hourly radiotelemetry

80

Carolina. However, the numbers of amphibians migrating 60

into and out of ponds during breeding and metamorphos-40

ing events varies considerably among species and years.

The salamander Ambystoma opacum, for example, did 20

not enter or leave a small pond in South Carolina from 0

1970 to 1980, but in 1987, nearly 300 adult females <1

1–5

5–10

>30

entered and more than 800 metamorphs exited the pond entered and more than 800 metamorphs exited the pond.

10–15

15–20

20–25

25–30

Distance moved (m)

In the same pond over a 12-year period, patterns of movement among species were not concordant (Fig. 8.14).

FIGURE 8.12 The snake Enhydris plumbea in Malaysia (Borneo) moves very little. The method of collecting movement data influences Mass movements of amphibians often result in high mor-the results and might lead to misleading conclusions in species that move tality caused by automobile traffic. Although a few parks considerable distances. Adapted from Voris and Karns, 1996.

and recreation areas now construct fencing and under-ground passages for migrating amphibians, the migratory biology of amphibians and other animals is usually not considered when designing roads.

capture site, which indicates that they are capable of ori-Sea turtles and large freshwater turtles (Podocnemis) entation. Because the displaced salamanders climbed up arrive at nesting beaches by the hundreds over a few on vegetation, airborne chemical cues were implicated nights. Garter snakes and rattlesnakes enter and leave in orientation. Homing studies on Desmognathus fuscus hibernacula in large groups. Thus mass movements are in Pennsylvania add support to the hypothesis that chem-common and generally appear related to breeding events ical cues are involved in homing. These salamanders or overwintering. These and the preceding examples maintain small home ranges along a stream for extended largely represent directed and cyclic movements away time periods. Four groups of salamanders were displaced from the home ranges used during the activity season.

to discover the possible cues used in homing behavior: One group was a normal, nontreated group; the second was an anosmic (olfactory system nonfunctional) group; Dispersal

the third group was blind; the fourth group was a sham-treated control group. The anosmic group did not return Dispersal is undirected movement to locations unknown by to original home ranges, whereas varying numbers of the dispersing unknown by to original home ranges, whereas varying numbers of the dispersing animal and commonly refers to juveniles the other treated groups did return, lending support to leaving the home ranges of their parents to find a home the hypothesis that chemical cues are involved in the ori-of their own. Habitat instability, intraspecific competition, entation and homing process.

and inbreeding depression are considered the primary evo-Among the most striking movements by extant lutionary driving forces resulting in dispersal (Fig. 8.15).

amphibians and reptiles are sea turtle migrations from Whether or not individuals should disperse is based on hatching site to feeding grounds as juveniles and, many the relative costs and benefits of doing so. Costs to years later, back to nesting beaches as adults. Green sea dispersal include increased predation risk associated with turtles, Chelonia mydas, emerge from eggs at Tortu-entering unknown and unfamiliar habitats, potential diffi-guero, Costa Rica, enter the Caribbean Sea, and migrate culties finding resources (food, shelter), and potentially

GULF OF MEXICO

Florida

ATLANTIC OCEAN

Yucatan

CUBA

Bay of

Campeche

Haiti Dominican

Puerto Rico

Jamaica

Republic

MEXICO

BELIZE

HONDURAS

GUATEMALA

CARIBBEAN

EL

SALVADOR

SEA

NICARAGUA

COSTA RICA

PANAMA

VENEZUELA

COLOMBIA

PACIFIC OCEAN

FIGURE 8.13 Green sea turtles travel from their nesting beaches throughout the Caribbean Sea to reach beaches as far north as Cuba. Adapted from Bowen and Avise, 1996.

3000

12000

300

1200

Ambystoma talpoideum Ambystoma tigrinum 10000

1000

2000

8000

200

800

6000

600

1000

4000

100

400

2000

200

0

0

0

0

79 80 81 82 83 84 85 86 87 88 89 90

79 80 81 82 83 84 85 86 87 88 89 90

juvenilesg

1000

10000

8000

500

Ambystoma opacum Pseudacris ornata Breeding females

800

8000

400

6000

Metamorphosin

600

6000

300

4000

400

4000

200

2000

200

2000

100

0

0

0

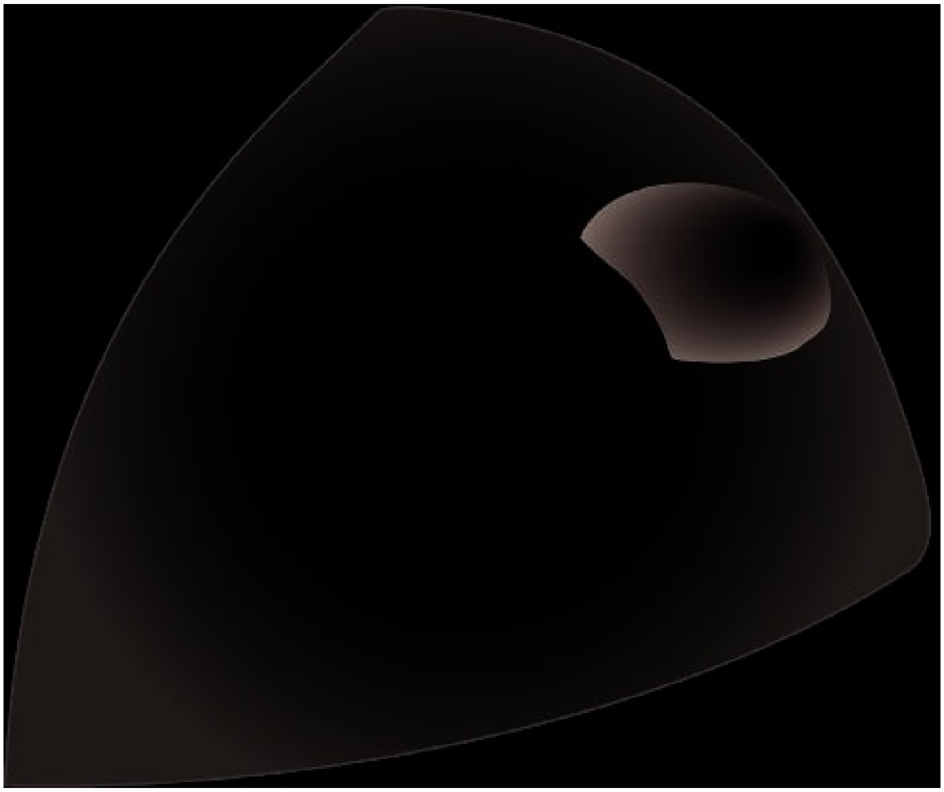
0

79 80 81 82 83 84 85 86 87 88 89 90

79 80 81 82 83 84 85 86 87 88 89 90

Year

FIGURE 8.14 The number of breeding females and metamorphosing larvae of three salamander species and one frog species varies impressively from year to year in the small Carolina bay, Rainbow Bay, in South Carolina. Migration patterns of amphibians using the same breeding sites are not synchronous. Adapted from Pechmann et al., 1991.



Costs (–) and Benefits (+) of Dispersal Intraspecific

competition

dispersal

favored

local competition

+

competition among relatives

0

local competition

philopatry

competitive ability

favored

–

helping behaviors

Habitat

–

0

+

–

0

environmental quality

+

environmental instability

common suitable patches

Inbreeding

environmental quality

environmental stability

inbreeding depression

scarce suitable patches

heterozygous advantage

outbreeding depression

FIGURE 8.15 Model showing the relationships between costs and benefits of dispersal. The curved surface represents points where costs and benefits of dispersal are at equilibrium. Dispersal behavior will be selected above the plane, whereas philopatry will be selected below the plane. The three-dimensional volume represents a species in which some individuals (e.g., juveniles) disperse and others (e.g., adults) remain where they are.

Adapted from Clobert et al., 1994.

increased aggression from unfamiliar conspecifics. Bene-survivors will be the individuals with the best set of char-fits include opportunities to discover better resources, acteristics for the poor environment. By not dispersing increased likelihood of outbreeding, and potentially and mating with other individuals that survived and thus reduced local competition. In populations of the European carry traits for survival under poor conditions, individuals lizard Lacerta vivipara, more than 50% of juveniles dis-with traits associated with success in the poor habitat will perse, whereas very low numbers of yearlings or adults dis-be favored. Even though inbreeding is potentially high, perse.

Dispersal

of

juveniles

is

greater

when

the inbreeding is selective, and as a consequence, typical population density is high in their population of origin.

costs of inbreeding are relaxed compared with benefits High population density is an indicator of a temporally juveniles gain by remaining in their place of origin (philo-high-quality environment. High-quality environments pro-patry). In this example, a complex interaction between var-duce offspring that are better able to compete because of iation in the local environment and the costs and benefits relatively larger size and condition. By dispersing, these of dispersal with respect to inbreeding determines whether juveniles offset disadvantages associated with inbreeding.

juveniles should or should not disperse.

In low-quality environments, only the most competitive Amphibian metamorphs and hatchling sea turtles are juveniles will survive, whether or not they disperse. These two examples of cohorts that leave their natal sites but will

return in subsequent years to breed. They do not appear to HOMING AND ORIENTATION

know where they are going as hatchlings, but innate navigational mechanisms will allow them to return later in life.

Homing refers to the ability of displaced individuals to Metamorphosing amphibian larvae move into and return to their original location. Implicit in any discus-through the habitat of their parents, most becoming part sion of homing is the idea that animals must be able to of the local populations. Dispersal distance usually is sense the direction they are moving. Amphibians and small, and the juveniles occupy home ranges in vacant reptiles that migrate, particularly during breeding events spots among adults or in peripheral locations. Similar dis-or just before and after overwintering, generally do not persal occurs in reptiles and direct-developing amphibians, move randomly. Amphibians migrating into and out of although dispersal can occur later as large juveniles make breeding ponds enter and leave by relatively predictable the transition into the breeding population.

pathways, as do rattlesnakes moving to overwintering Several species of frogs in unrelated clades transport den sites. Orientation can involve visual frogs in unrelated clades transport den sites. Orientation can involve visual, olfactory, audi-their eggs, and subsequently either their tadpoles or juve-tory, or even magnetic cues, each of which requires a niles, on their backs. Most dendrobatids and aromobatids different system for reception (Fig. 8.17). Orientation drop off their litter of tadpoles in one place (Fig. 5.17), requires some sort of map and a compass. If the compass but some, such as Ranitomeya vanzolinii, drop individual is based on celestial cues such as the sun, then a clock is tadpoles in different places (Fig. 9.19). Sphenophryne cor-necessary to reset the compass as the sun's azimuth nuta, a microhylid from Australia, transports its young, changes seasonally.

dropping them off periodically (Fig. 8.16). Other frogs Salamanders generally cannot home for more than that carry their young on their backs, such as Stefania about 30 meters, but the newt Taricha rivularis in Califor-evansi (Fig. 5.19), may drop off young in different places nia can home for up to 2 km. Some individuals can home as well. Although these behaviors are usually considered from about 8 km. Some turtles can home from only in the context of parental care and reproductive modes, 0.5–1 km (Clemmys guttata), but others home over they certainly play a role in dispersion as well.

500 km (sea turtles). Crocodylians can home for up to Among animal species with polygynous mating sys-2 or more km. In the few lizards studied, relocation to dis-tems, males generally disperse farther than females, partly tances of about 200 m or less result in good homing abil-because males compete for females and partly because ity, but at a greater distance, the lizards do not return.

females often disperse less as the result of their association Many amphibians and reptiles return to specific shel-with resources or refugia from predators. Male Uta stans-ters following both short-and long-distance movements.

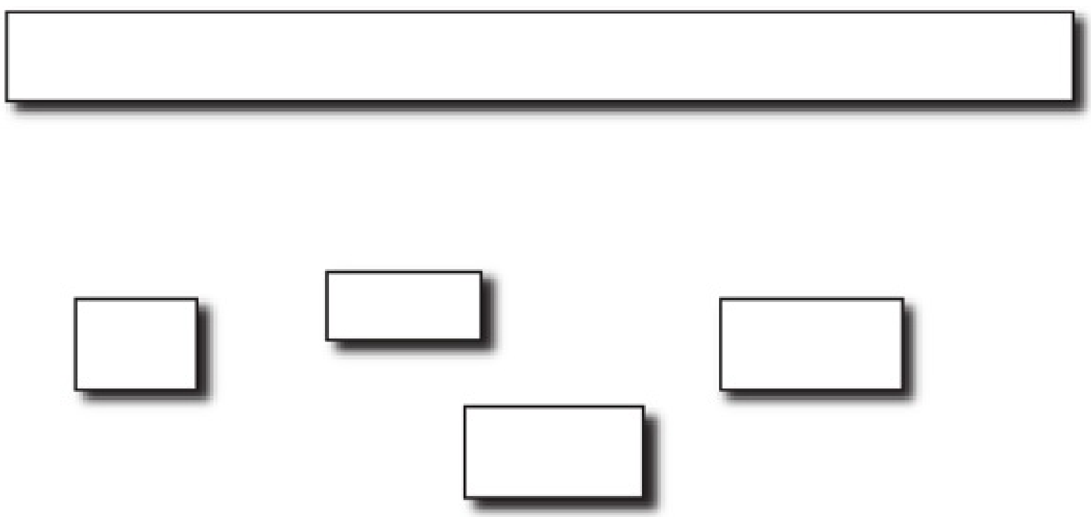
buriana disperse during their first year of life, but in some Movements of the snake Coluber viridiflavus in Italy can cases, females disperse equally as far as males. Females be divided into single-day loops in which the snake leaves appear to disperse until they locate good territories. Some its shelter and returns by the end of the day, complex males disperse farther than females because they have to loops in which the snake moves greater distances over go farther to find unoccupied territories.

several days using temporary shelters, and large loops involving movements up to 3 kilometers and lasting up to a month. Single-day loops are primarily excursions for basking, complex loops appear to be associated with foraging, and large loops appear associated with reproductive activity (Fig. 8.18).

Landmarks

Within home ranges, most amphibians and reptiles use local landmarks. The repeated use of the same perches, foraging areas, and overnight retreats indicates that individual reptiles and amphibians recognize landmarks within their home ranges. The existence of home ranges and territories is also evidence for the ability of individuals to recognize local landmarks. On a larger spatial scale, many species appear able to recognize the kinds of habitats they live in and orient to those. Some Anolis FIGURE 8.16 Some amphibians carry their tadpoles or young around lizards are known to use elevated vantage points to survey and aid in their dispersal. The Australian microhylid, Sphenophryne their immediate habitat. In a simple but effective experi-cornuta, drops off its young in different places. Photograph by Stephen J. Richards.

ment, three species of Anolis were placed on artificial



Pond

Local odor

Sun, moon, stars,

Fixed, visual

Earth's

Earth's

Chorus of

odors

patterns

skylight polarization

landmarks

magnetic field

conspecifics

Eyes and

Magneto—

Olfactory System

Auditory system

pineal complex

reception

Clock

Map

Piloting

Compass

FIGURE 8.17 Relationships among cues, sensory systems, and the mechanistic basis of orientation and navigation for anurans. These relationships may be similar for most amphibians and reptiles. For terrestrial species, odors might be associated with den sites or daily retreats. Adapted from Sinch, 1990.

elevated posts from which they could see two vegetation July 6

Sept 10

types, a grass–bush habitat and a forest habitat. Anolis July 12

auratus and A. pulchellus choose the grass–shrub habitat, May 2

1100

Male # 9

whereas A. cristatellus choose the forest habitat. Because May 7

June 28

Aug 9

the choices correspond with the natural habitats of the Sept 4

lizards, the study reveals that these species used the 1000

habitat structure as a landmark or cue to direct their Female # 8

movement.

Orientation and homing ability varies among lizards, 900

June 23

even in the same habitat. In open habitats of southern June 14

Aug 16

Idaho, horned lizards, Phrynosoma douglassi, seem unable y (m)

May 23

May 7

800

June 2

to find their original home range when displaced, yet adult Aug 20

sagebrush lizards, Sceloporus graciosus, are able to orient toward and return to their original home ranges. Horned May 21

700

Sept 11

lizards may not maintain home ranges for long because May 15 Aug 22

their movements follow the movements of their ant prey.

May 10

Aug 20

Sept 5

July 8

July 8

Because home range and defense of all or part of the home 600

July 4

May 4

July 1

July 27

range (territories) is ancestral in lizards, horned lizards Female # 11

have lost the ability to orient and return to home ranges.

When disturbed, many amphibians and most reptiles 300

400

500

600

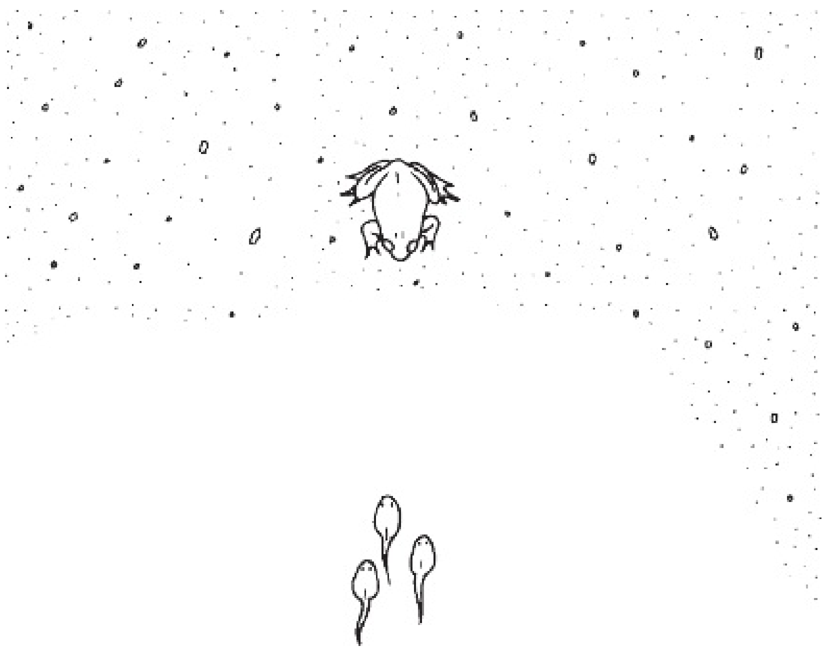
700

rapidly retreat along what appear to be well-known escape x (m)

routes. This too demonstrates their familiarity with local FIGURE 8.18 Movement activity of three individual Coluber viridifla-landmarks. Directed long-distance movement, such as vus. Short arrows indicate typical 1-day or complex movements, and the annual migrations of prairie rattlesnakes to den sites, also heavier, long arrows indicate large loops. The tip of each arrow indicates suggests the importance of local landmarks in orientation the most distant point reached by the snake during each excursion.

Adapted from Ciofi and Chelazzi, 1994.

and navigation.



x–y Orientation

Orientation by Polarized Light

The interface between aquatic (or marine) and terrestrial Light radiates outward from the sun. As the light waves environments provides a landmark for orientation by enter the earth's atmosphere, the atmosphere deflects animals that use the interface. Many frogs, for example, some light waves into a plane perpendicular to the original typically jump into the water at approximately 90 to plane of entry. This scattering or deflection is polarization, the shoreline—their jumps are nonrandom with respect and the scattered component (i.e., polarized light) travels to physical characteristics of the environment. The in a single plane along a path called the e-vector. Because advantages to orientation toward or away from shore-the e-vector always remains perpendicular to the sun-lines are clear. For adult amphibians that sit along the light's entry plane rather than the earth's surface, the ori-shore, escape into the water is important for avoiding entation of the e-vector plane relative to every spot on terrestrial predators; for larvae facing metamorphosis, earth changes constantly as the earth rotates. For amphi-orientation toward shore is critical for emergence into bians or reptiles that see polarized light, this changing ori-the terrestrial environment; for adults during breeding entation offers a directional clue. In addition, an inverse migrations, orientation toward breeding sites is crucial relationship exists between reflection and polarization: to find aquatic environments for egg deposition. This Over water surfaces and damp soils, reflectance is low type of orientation is termed y-axis orientation. Linear and polarization is high; over drier soils, reflectance is cliff faces, riverbanks, and a host of other physical high and polarization is low. Variation in polarized light characteristics of the environment might also serve as over wet versus dry landscapes provides amphibians and the basis for x–y orientation in terrestrial species. For reptiles with means to differentiate between wet and dry aquatic amphibians, the x axis is the shoreline and the areas and to move to their preferred habitat.

amphibians tend to move perpendicular (90, the y axis) Much indirect evidence and some clever laboratory to it (Fig. 8.19). Of course, shorelines can face any direc-experiments suggest that some amphibians and reptiles tion. For example, a circular pond has sections that face use polarized light in orientation and navigation. The emy-every possible direction of the compass. Amphibians use did turtle Trachemys scripta, when displaced on sunny the sun and its trajectory, which are predictable, to set days to terrestrial sites 300 meters away from their home their x–y compass based on the particular shoreline that ranges in a pond, orient toward the pond even though they they use. When landscape views are taken away, frogs cannot see it. On cloudy days, turtles fail to orient, indicat-and tadpoles retain their ability to orient perpendicular ing that the clouds, which stop polarized light, interfere to the x axis as long as they can view the sky. Some with the ability of turtles to orient. The outer segments evidence suggests that turtles may also use the sun to of cones in the eyes of T. scripta are capable of differen-set an x–y compass.

tially absorbing polarized light, further suggesting that the mechanism for locating ponds may be detection of polarized light reflected from aquatic habitats.

The pineal body of salamanders and possibly lizards is a y-axis

polarized light receptor. Both blinded and normal-sighted Ambystoma tigrinum orient to a shoreline once their internal compass has been set based on a vector of polarized light.

When light is blocked from the top of the head by opaque plastic, these salamanders orient incorrectly, thus implicat-ing the pineal in orientation based on polarized light.

Although little research has been conducted on use of x-axis

polarized light by lizards, some recent work on Sleepy lizards (Tiliqua polarized light by lizards, some recent work on Sleepy lizards (Tiliqua rugosa) by Michael Freake suggests that 90°

Sleepy lizards are able to use celestial cues to orient, allow-ing them to determine the compass bearing of movements.

Covering the parietal eye interfered with the lizard’s ability to orient even though the lateral eyes were unobstructed and provided them complete access to visual cues (includ-FIGURE 8.19 Y-axis orientation is a type of celestial orientation. The ing celestial cues and landmarks). Consequently, it appears animal establishes a homing axis (y) perpendicular to an identifiable that Sleepy lizards use the parietal eye to detect polarized physical attribute of its home (e.g., shoreline, the x axis). Normal escape light to set a directional compass that allows them to response is into the pond for the frog being approached by terrestrial navigate without the use of cues detected by lateral eyes.

predators or to shallow water for tadpoles being approached by aquatic predators; return follows the compass direction of the y-axis. Adapted This phenomenon may be much more widespread among from Adler, 1970.

squamate reptiles than previously thought.

Orientation by Chemical Cues

cues serve as orientation and navigation cues. Early studies on Taricha rivularis, in which salamanders were rendered Many habitats (e.g., ponds) and retreat sites have character-anosmic by damaging the olfactory nerves, caused a reduc-istic odors that can be used by amphibians and reptiles for tion in the homing ability, thus demonstrating that the olfac-orientation and navigation. In southern California, the toad tory system is involved in orientation. The salamander Anaxyrus boreas breeds during spring in ponds and lakes.

Ambystoma maculatum migrates on cloudy and rainy nights The toads spend the remainder of the year dispersed in yet locates ponds. A clever experiment, in which salamanders the surrounding terrestrial environment. When displaced were placed in arenas with two paper towels, one soaked in 50–200 meters from a pond on clear nights, adults orient to water and mud from their home pond and the other soaked the pond and return; on cloudy nights they also orient to the with water and mud from nonhome ponds, revealed that A.

pond but not as precisely. Blinded toads also orient to the maculatum discriminates between the two odor sources, pref-pond, but the possibility exists that they use alternate light erentially orienting toward the odor from their home pond.

receptors. However, when olfactory nerves are severed and These results are consistent with field observations that when the toads rendered anosmic, the toads orient randomly on individuals of A. maculatum are placed in unfamiliar ponds, clear nights even though celestial cues are available. Thus, they often migrate back to their home pond.

even in the presence of celestial cues, loss of olfactory senses removes the toads' ability to orient. Because a host of environ-Magnetic Orientation mental factors can affect the dispersion of chemical cues in natural habitats (e.g., wind), it is likely that, once chemical The eastern red-spotted newt (Notophthalmus viridescens) cues are detected, they are used to set an internal compass.

is well known for its accurate homing behavior. This newt Once the compass course is set by chemical cues, frogs can apparently detects its geographic position based on informa-use celestial cues to navigate.

tion associated with its home site (i.e., a "map") and a sense Olfactory cues also appear important in orientation and of direction ("compass"). One possible basis for such a map navigation in some salamanders. Observations that salaman-is the spatial variation in the magnetic field. The newts may ders retain the ability to home accurately without celestial have two different magnetoreception mechanisms that cues suggest that olfactory cues are used, particularly on explain differences between their orientation responses to overcast or rainy nights. Displaced Plethodon jordani that shoreline and their home pond under different conditions are blinded return to home sites, suggesting that olfactory of light (Fig. 8.20). One mechanism involves visual centers Orientation to shore

Orientation to pond (home)

Shore

Shore

Home

Home

Full

Short

Full

Short

spectrum

wavelength

spectrum

wavelength

similar

similar

similar

different

similar

different

Shore

Shore

Home

Home

Long

Long

wavelength

wavelength

Full

Full

No orientation

spectrum

spectrum

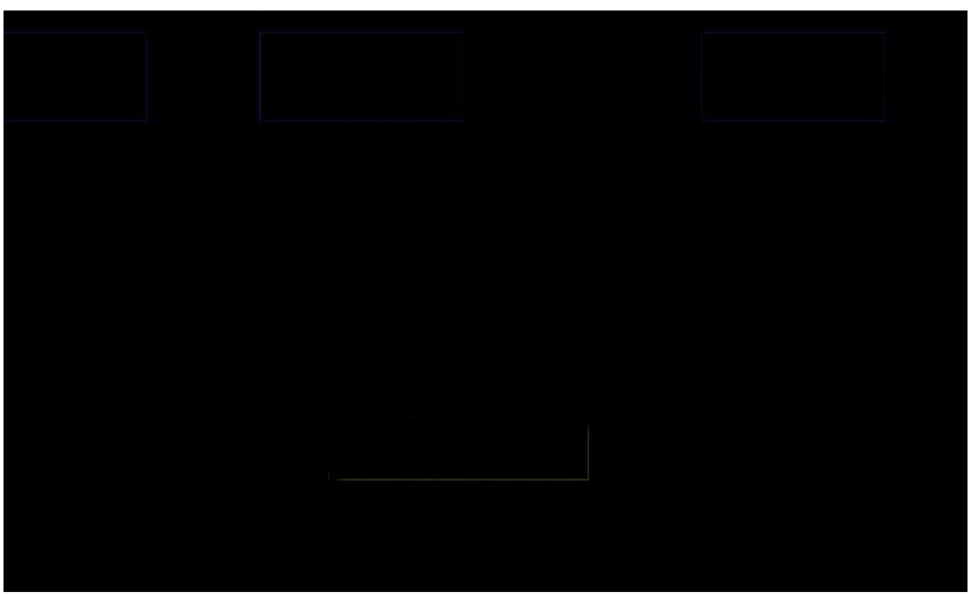
(random)

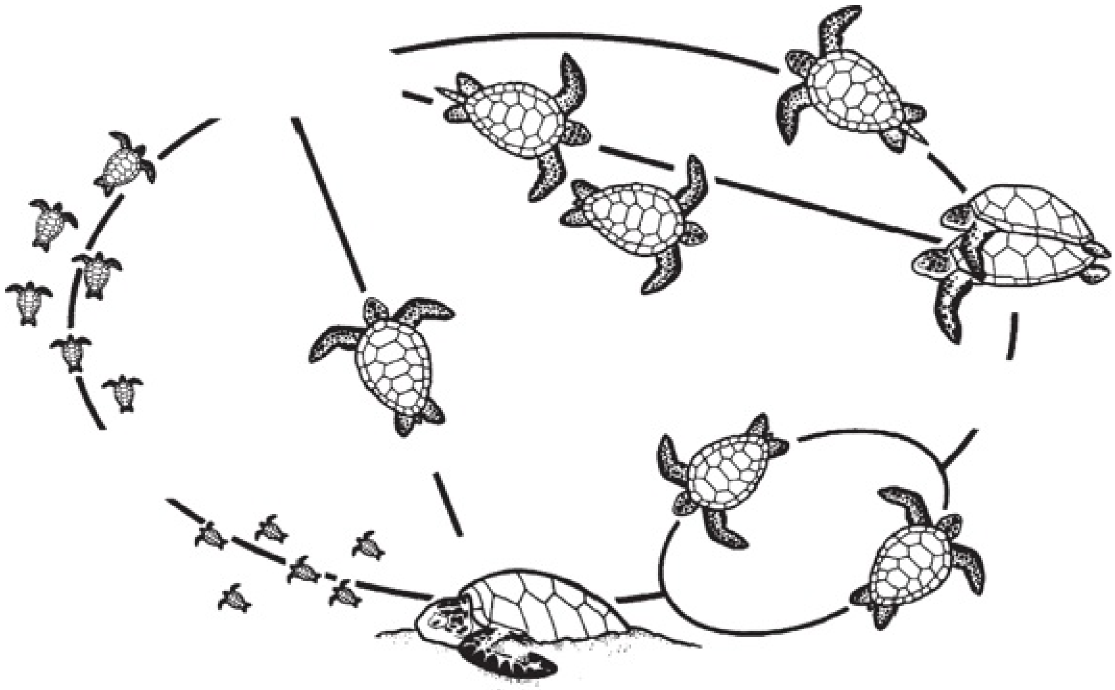
different

different

FIGURE 8.20 Diagrammatic summary of experiments on orientation toward shore and toward the home pond for eastern red-spotted newts. In both sets of experiments, controls are those with a full spectrum of light available.

In the left panel, newts oriented toward shore in both of the controls and when under short wavelength light. Under long wavelength light, newts oriented approximately 90 counterclockwise from the shore, and their pattern of orientation was significantly different from both their control and the newts under short wavelength light, demonstrating the light dependency of shoreline magnetic orientation. In the right panel, newts oriented toward their home ponds in both controls and under short wavelength light but oriented randomly under long wavelength light, demonstrating the light dependency of home pond magnetic orientation. Adapted from Phillips and Borland, 1994.





in the brain that appear to respond to directional magnetic cues. When leaving the beach following hatching, the stimuli. Because visual centers are involved, this mecha-hatchlings first orient on light from the moon and stars nism depends on light. The other mechanism involves the reflecting off the ocean, which takes them to the water.

trigeminal nerve system, which is independent of visual Once in the water, they orient on incoming waves and input and thus does not require light. The possibility exists move perpendicular to them, which carry them out to sea that a highly sensitive magnetite-based receptor responds (Fig. 8.21). When the small turtles intersect the Gulf to polarity of the magnetic field, and if present in newts, Stream, currents carry them around the Sargasso Sea would explain their ability to home. Such receptors have (Fig. 8.22). Magnetic cues appear to be used for been found in other vertebrates.

Alligators and sea turtles appear capable of orienting on the basis of magnetic cues as well. Sea turtles are Visual

Wave

Magnetic

renowned for their keen abilities to navigate, and because cues orientation

orientation

much of their environment is open ocean, landmarks are largely unavailable. Loggerhead sea turtles (Caretta car-etta) that hatch in Florida, for example, appear to circle the North Atlantic Ocean and return several years later as juveniles to the American coastline. One population of green sea turtles (Chelonia mydas) nests on beaches of Ascension Island, more than 2200 km east of their feed-Wave direction ing grounds off the coast of Brazil. The regular return of adults to the tiny island attests to their capability for precise orientation and navigation. Studies on mitochondrial DNA have shown that females in this population and other Beach

Wave refraction

Open ocean

zone

populations return to the beaches where they hatched.

FIGURE 8.21

Magnetic orientation likely is involved in open ocean nav-Different orientation cues believed to guide hatchling Loggerhead sea turtles from their nests on beaches in Florida to the open igation. In laboratory experiments, hatchlings orient to ocean. Lines indicate direction of waves. Adapted from Lohmann et al., magnetic fields, to wave action, and even to chemical 1997, and Russel et al., 2005.

Adult males return

to foraging areas

COASTAL SHALLOW WATER ZONE

BENTHIC FORAGING ZONE

immature turtles—adult turtles

Developmental migration

Age at first breeding

about 30–50 years

Adult males and females

Adult males and females

migrate to mating areas

MATING AREA

Breeding migration

at 2–8 year intervals

SHALLOW WATER

INTERNESTING HABITAT

adjacent to nesting beach

OPEN OCEAN

Adult females

SURFACE FORAGING ZONE

return to foraging areas

“lost years” 5–20 year duration

hatchlings

2-week

intervals

NESTING BEACH

Eggs

8–10 weeks incubation

FIGURE 8.22 Life cycle of the green sea turtle showing the course of movements throughout life and possible cues used for orientation during each life history stage. Adapted from Miller, 1996.

navigation while at sea. Once they reach maturity, at an REFERENCES

age of 30–50 years, the adult females return to beaches for nesting.

Introduction

Broadley, 1978; Greene, 1997; Lee, 1975; Pianka and Parker, 1975; Vanzolini et al., 1980; Whitford and Bryant, 1979; Whiting et al., 1993; QUESTIONS

Williams, 1969.

General

1. Using a reptile or amphibian species of your choice, Galbraith et al., 1987; Gibbons, 1986; McIntyre and Wiens, 1999.

discuss why you might expect the home range of a Local Distribution of Individuals male to be larger than the home range of a female Home Ranges

during the breeding season.

Alexy et al., 2003; Anderson, 1993; Aresco, 1999; Auffenberg and Franz, 2. When different methods were used to examine 1982; Bodie and Semlitsch, 2000; Boglioli et al., 2000; Bull and movement in the Malaysian snake Enhydris plumbae, Baghurst, 1998; Butler et al., 1995; Diemer, 1992; Doody et al., the results were different. What were these different 2002; Duvall et al., 1985; Epperson and Heise, 2003; Eubanks methods and how do you explain the differing et al., 2003; Hall and Steidl, 2007; Ligon and Stone, 2003; Madsen, results?

1984; Madsen and Shine, 1996; Mills et al., 1995; Morafka, 1994; 3. Describe movements in the life cycle of the Green sea Peterson and Stone, 2000; Pike, 2006; Plummer and Shirer, 1975; Rose, 1982; Ruby, 1978; Smith et al., 1997; Stamps, 1978, 1983; turtle and discuss orientation cues used by juveniles, Stone, 2001; Tiebout and Gary, 1987; Van Loben Sels et al., 1997; immatures, and adults.

4

Webb and Shine, 1997; Wilson et al., 1994.

. What is the difference between landmark orientation Territories

and x–y orientation and what are real examples of Brown and Orians, 1970; Bunnell, 1973; Deleˆtre and Measey, 2004; each?

Howard, 1978a,b; Jaeger, 1981; Jaeger et al., 1982; McVey et al., 1981;

Shedahl and Martins, 2000; Simon, 1975.

Evolution of Territoriality

ADDITIONAL READING

Martins, 1994, 2002; Stamps, 1977.

Other Patterns of Space Use

Adler, K. (1970). The role of extraoptic photoreceptors in amphibian Aleksiuk and Gregory, 1974; Anderson, 1967; Brodie et al., 1969; Cald-rhythms and orientation: a review. Journal of Herpetology 4: well, 1989; Congdon et al., 1979; Duellman and Trueb, 1986; Gehl-99–112.

bach et al., 1969; Guillaume, 2000a,b; Marquis et al., 1986; Wells Bruce, R. C., Jaeger, R., and Houck, L. D. (Eds.) (2000). The Biology of and Wells, 1976.

Plethodontid Salamanders. Kluwer Academic/Plenum Publishers, New York.

Movements, Homing, and Migrations Clobert, J., Massot, M., Lecomte, J., Sorci, G., Fraipont, M., and Bar-Anderson and Karasov, 1981; Barthalmus and Bellis, 1972; Bentivegna, bault, R. (1994). Determinants of dispersal behavior: the common 2002; Dodd and Byles, 2003; Godley et al., 2002; Huey and Pianka, lizard as a case study. In Lizard Ecology: Historical and Experimen-1981; Madison and Shoop, 1970; Pechmann and Semlitsch, 1986; tal Perspectives. L. J. Vitt and E. R. Pianka (Eds.), pp. 183–206.

Pilliod et al., 2002; Schabetsberger et al., 2004; Secor, 1994; Sem-Princeton University Press, Princeton, NJ.

litsch, 1981; Stickel, 1950, 1989; Tuberville et al., 1996; Voris and Dingle, H. (1996). Migration. Oxford University Press, Oxford.

Karns, 1996.

Gauthreaux, S. A. Jr. (Ed.). (1980). Animal Migration, Orientation, and Mass Movements Navigation. Academic Press, London.

Clevenger et al., 2002; Gibbons and Bennett, 1974; Pechmann et al., Lutz, P. L., and Musick, J. A. (Eds.). (1996). The Biology of Sea Turtles.

1991.

CRC Press, Boca Raton, FL.

Dispersal

Russel, A. P., Bauer, A. M. and Johnson, M. K. (2005). Migration in amphibians and reptiles: An overview of patterns and orientation Clobert et al., 1994; Doughty et al., 1994; Stamps 1983.

mechanisms in relation to life history strategies. In Migration of Homing and Orientation

Organisms: Climate, Geography, Ecology (A. M. T. Elewa (Ed.).

Adler, 1976; Adler and Phillips, 1991; Adler and Taylor, 1973; Bowen Springer Publishing, New York.

and Karl, 1996; Ciofi and Chelazzi, 1994; Coulson, 1974; Diego-Stamps, J. A. (1983). Sexual selection, sexual dimorphism, and territo-Rasilla, 2003; Dodd, 1994; Dodd and Cade, 1998; Ferguson, 1967, riality. In "Lizard Ecology: Studies of a Model Organism" (R. B.

1971; Freake, 1998, 1999; Gibbons and Smith, 1968; Goodyear, Huey, E. R. Pianka, and T. W. Schoener, Eds.), pp. 169–204. Har-1971; Goodyear and Altig, 1971; Grant et al., 1973; Grassman vard University Press, Cambridge.

et al., 1984; Guyer, 1991; Irwin et al., 2004; Johnson, 2003; Kiester Wells, K. D. (2007). The Ecology and Behavior of Amphibians. Univer-et al., 1975; Liebman and Granda, 1971; Lohmann, 1992; Lohmann sity of Chicago Press, Chicago.

et al., 1996, 2001, 2004; Madison, 1969; Martins, 1994; McGregor Wilson, J. (2001). A review of the modes of orientation used by amphi-and Teska, 1989; Phillips et al., 2001; Rodda, 1984, 1985; Rodda bians during breeding migration. J. Pennsylvania Academy of and Phillips, 1992; Shoop, 1968; Taylor and Adler, 1973; Tracy, Sciences 74: 61–66.

1971; Tracy and Dole, 1969; Yeomans, 1995.

Chapter 9

Communication

and Social Behavior

Communication

Reproductive Behavior

Miscellaneous Social Aggregations Caecilians

Mating Systems

Questions

Salamanders

Alternative Mating Strategies

Additional Reading

Frogs

Sexual Dimorphism and Sexual

References

Turtles

Selection

Crocodylians

Tuataras and Lizards

Snakes

Every organism constantly interacts with other organisms.

recognize a high-quality male among the numerous calling The interactions include predation, feeding, physiological males and select the “best” one. Signal production has an responses to disease organisms, and numerous others. Social energetic cost, but further, it has a potential life-threatening behavior is an interaction with one or more conspecifics, cost. If a conspecific can locate another conspecific by the that is, individuals of the same species and, occasionally, communication signal, so can a predator. In the Neotropics, between individuals of different species. Social interactions one group of predaceous bats locates male frogs by “homing may be a regular feature of an individual’s daily life, partic-in” on the frog’s advertisement call.

ularly for individuals living in groups or occupying adjacent Social interactions are integral to an individual’s sur-territories, or they may occur once a day, once a week, and vival and ultimately influence an individual’s evolutionary even only once a year during the reproductive season in a fitness.

The diversity of amphibians and reptiles has again low-density species. Whatever their frequency, social inter-allowed many species to serve as model organisms for the actions require some form of communication. Amphibians study of the evolution of communication and social behav-and reptiles communicate through a variety of senses: visual, ior. The focus in this chapter is first communication and chemical (nasal and vomeronasal), acoustic, and tactile.

then sexual behavior because interactions and an indivi-In many instances, communication involves more than one dual's choices associated with mate choice have a more sense working together, synchronously, or sequentially.

immediate and direct effect on individual fitness than a The evolution of an organism's signal production is inti-decision or interaction in the context of other types of mately interwoven with the evolution of its signal receptors.

social behavior. Other aspects of social behavior are pre-One system cannot change without adjustments in the other, sented in Chapters 4, 10, and 11.

or communication is lost and interactions fail. Frogs have an impressive array of vocalizations, most of which are used for mate attraction. Frogs have an equally impressive and COMMUNICATION

sophisticated acoustic reception system that allows them to discriminate among species and among individuals. Skinks Strictly speaking, communication is defined as "the coop-and other scleroglossan lizards can recognize conspecifics erative transfer of information from a signaler to a and often individuals exclusively by chemical cues. The pri-receiver." Consequently, if a male frog calls and his call mary benefit of high-resolution communication is the ability is not received by another frog, or a snake produces chem-to identify and locate mates in a complex environment, such ical cues that are not detected by another snake, communias a multispecies frog chorus in a densely vegetated marsh, cation has not occurred. Further, most signal and reception and to discriminate critically among mates, that is, to systems of reptiles and amphibians are controlled by Herpetology, 3rd Ed.

sex hormones and, thus, are most effective during the reproductive condition. Most studied reptiles have color breeding season.

vision, which further suggests that color is used in Visual communication uses either body movement or communication.

a series of movements or the flashing of a body part Acoustic communication is best known in anurans, but having a distinctive color or shape. In amphibians and crocodylians, some turtles, and some lizards (Gekkonidae) reptiles, limb movements, head bobs, rapid shuttling regularly use sound (Table 9.1). Sounds for social com-movements, and open-mouth threats comprise the most munication are produced by rubbing body parts together common signals. Visual communication is best known (some gekkonids, some viperids) and slapping the body for iguanian lizards but occurs in many other amphibians against surfaces such as water (crocodylians), although and reptiles, often in combination with other signals.

vocal sounds are most prominent. These sounds (vocali-Although visual displays are most often directed at zations) are produced by airflow over the vocal specific individuals, assertion or advertisement displays cords. Many frogs have vocal sacs to enhance sound can be performed by territorial males to reinforce their transmission.

territory status to all males or to attract females within Chemical communication uses odors that are derived sight. Among reptiles, the combination of an approach from glandular secretions, either volatile ones (nasal) or with head bobs occurs in so many groups that it likely is surface-adherent ones (vomeronasal). Chemical communian ancestral trait and may reflect an ancient solution to cation has been studied most intensely in salamanders and the identification of gender and conspecifics at a skinks. It is used widely by other scleroglossan lizards distance. Many reptile species are sexually dimorphic in (includes snakes) and by some iguanians. Although few coloration, suggesting the importance of color in species studies are available, chemical communication is probably and gender recognition. Because some seasonal color used during reproduction and other social interactions changes are tied to reproductive events and under the con-in caecilians and in at least one clade of frogs, the trol of androgens, color also signals an individual's Mantellidae. In amphibians and reptiles, most chemical TABLE 9.1 Vocalizing

Mantellidae. In amphibians and reptiles, most chemical TABLE 5.1 Vocalizing Taxa of Amphibians and Reptiles, Exclusive of Anurans.

Taxon

Frequency

Taxon

Frequency

Ambystomatidae

+

*Sphenodontidae

+++

Ambystoma maculatum

Amphiumidae

+

Agamidae

+

Cryptobranchidae

++

Brachysaura minor

Andrias davidianus

Anguidae

+

Dicamptodontidae

++

Ophisaurus

Dicamptodon ensatus

Chamaeleonidae

+

Plethodontidae

++

Chamaeleo goetzei

Aneides lugubris

Cordylidae

+

Salamandridae

+

Cordylus cordylus

Triturus alpestris

*Eublepharinae

+++

*Sirenidae

++

Coleonyx variegatus

Siren intermedia

*Gekkoninae

+++

Gekko gecko

Gekko gecko

Testudines

+

Lialis burtonis

*Testudinidae

++

Geochelone gigantea

*Iguanidae

+

*Alligatoridae

+++

*Lacertidae

++

*Crocodylidae

+++

Gallotia stehlini

Gavialidae

+++

Scincidae

+

Mabuya affinis

Teiidae

+

Cnemidophorus gularis

Note: Families marked with an asterisk have one or more species presumably using vocalization for intraspecific communication. The frequency of vocalization within a family or higher group is subjectively estimated: +++, more than 50% of species; ++, moderate; +, rare, one or few species in a speciose group. Some examples of voiced species are included.

Sources: salamanders through Triturus, Maslin, 1950; Siren, Gehlbach & Walker, 1970; turtles, Gans & Maderson, 1973; Geochelone, Frazier & Peters, 1981; crocodilians, Garrick et al., 1978; gharial, Whitaker & Basu, 1983; tuatara, Gans et al., 1984; Anolis, Milton & Jenssen, 1979; lizards, Bo¨hme et al., 1985.

communication relies on vomeronasal receptors, but gek-In plethodontid salamanders, mate location is aided by konoid lizards have well-developed nasal reception sys-

“nose tapping,” during which a male repeatedly touches tems (olfaction) that may function in communication.

his snout to the substrate. The snout bears a pair of naso-Odor-bearing chemicals are picked up by the tongue or labial grooves; these small grooves extend from the upper the surface of the head and transported to the nasal sac lip to the nares. Odors from the substrate move along the in amphibians and the roof of the mouth in reptiles and groove by capillary action and through the nares into the ultimately to the vomeronasal organ (Fig. 10.4). Croco-vomeronasal organ. In the hemidactyliines, each groove dylians and turtles lack vomeronasal organs, hence this extends to the tip of a small papilla (cirrus) that protrudes route for chemical communication is not available to from the lip beneath each naris.

them; however, both groups produce glandular secretions Courtship glands are most common in the Salaman-during the reproductive season and likely communicate dridae and Plethodontidae. Males of the eastern North chemically.

American newts (Notophthalmus) have a genial gland Tactile communication occurs when one individual on each side of the head. When a male encounters a rubs, presses, or hits a body part against another individreceptive female, he moves beside her and then performs ual. Tactile communication is common in turtles and a series of tail undulations that waft the pheromone snakes (e.g., ritualized combat in viperids) but also occurs toward her snout; shortly afterward, courtship continues commonly in amphibians and many lizards. Often, tactile and the female accepts the male's spermatophore. If a communication occurs after visual, acoustic, or chemical male finds an unreceptive female, he captures her by contact has been established. Because most species of clasping her neck with his enlarged hindlimbs. This amphibians and reptiles use a combination of signals dur-amplexus may last for 3 hours, and during this period, ing social communication, each group is reviewed the male places his genial glands against the female's separately.

snout. The glands' secretions induce the female's sexual receptiveness and allow courtship to proceed to spermatophore transfer.

Caecilians

Plethodontid salamanders have two general types of courtship glands, the mental gland on the chin and the cau-Most social communication in caecilians appears to be dal glands on the back at the base of the tail. The diverse

ductive cycle of the viviparous Mexican lizard Sceloporus lining? Biological Invasions 9: 445–452.

torquatus. Journal of Herpetology 27: 168–174.

Hahn, D. E., and Wallach, V. (1998). Comments on the system-Guillette, L. J., Jr., Arnold, S. F., and Mclachlan, J. A. (1996).

atics of Old World Leptotyphlops (Serpentes: Leptotyphlopi-Ecoestrogens and embryos—Is there a scientific basis for dae), with description of a new species. Hamadryad 23: concern? Animal Reproduction Science 42: 13–24.

50–62.

Guillette, L. J., Jr., Jones, R. E., Fitzgerald, K. T., and Smith, Hahn, W. E. (1967). Estradiol-induced vitellinogenesis and con-H. M. (1980). Evolution of viviparity in the lizard genus Sce-comitant fat mobilization in the lizard Uta stansburiana.

loporus. Herpetologica 36: 201–215.

Comparative Biochemistry and Physiology 23: 83–93.

Guimond, R. W., and Hutchison, V. H. (1972). Pulmonary, bra-Hahn, W. E., and Tinkle, D. W. (1965). Fat body cycling and chial, and cutaneous gas exchange in the mudpuppy, Nec-experimental evidence for its adaptive significance to ovarian turus

maculosus

maculosus

(Rafinesque).

Comparative

follicle development in the lizard Uta stansburiana. Journal Biochemisty and Physiology 42A: 367–392.

of Experimental Zoology 158: 79–86.

Guisan, A., and Hofer, U. (2003). Predicting reptile distributions Hairston, N. G. (1983). Growth, survival and reproduction of at the mesoscale: relation to climate and topography. Journal Plethodon jordani: Trade-offs between selective pressures.

of Biogeography 30: 1333–1343.

of Biogeography 30: 1233–1243.

Copeia 1983: 1024–1035.

Gundappa, K. R., Balakrishna, R. T. A., and Shakuntala, K.

Hairston, N. G., Sr. (1996). Predation and competition in sala-

(1981). Ecology of Ichthyophis glutinosus (Linn.) (Apoda, mander communities. In Long-term Studies of Vertebrate Amphibia). Current Science, Bangalore 50: 480–483.

Communities. M. L. Cody and J. A. Smallwood (Eds.).

Guttman, S. I. (1985). Biochemical studies of anuran evolution.

Pp. 161–189. Academic Press, San Diego.

Copeia 1985: 292–309.

Hall, B. K. (2007). Homoplasy and homology: Dichotomy or Guyer, C. (1991). Orientation and homing behavior as a measure continuum? Journal of Human Evolution 52: 473–479.

of affinity for the home range in two species of iguanid Hall, D. H., and Steidl, R. J. (2007). Movements, activity, and lizards. Amphibia-Reptilia 12: 373–384.

spacing of sonoran mud turtles (Kinosternon sonoriense) in Guyer, C., and Savage, J. M. (1987). Cladistic relationships interrupted mountain streams. Copeia 2007: 403–412.

among anoles (Sauria: Iguanidae). Systematic Zoology 35: Hallermann, J. (1994). Zur Morphologie der Ethmodialregion der 509–531.

Iguania (Squamata) – eine vergleichend-anatomische Unter-Gyi, K. K. (1970). A revision of colubrid snakes of the subfamily suchung. Bonner Zoologische Monographien 35: 1–133.

Homalopsinae. University of Kansas Publications, Musuem Hallermann, J. (1998). The ethmoidal region of Dibamus taylori of Natural History 20: 47–223.

(Squamata: Dibamidae), with a phylogenetic hypothesis on Haas, A. (2003). Phylogeny of frogs as inferred from primarily dibamid relationships within Squamata. Zoological Journal larval characters (Amphibia: Anura). Cladistics 19: 23–89.

of the Linnean Society 122: 385–426.

Haas, G. (1973). Muscles of the jaws and associated structures in Halliday, T. R. (1977). The courtship of European newts: An the Rhynchocephalia and Squamata. In Biology of the Repti-evolutionary perspective. In The Reproductive Biology of lia Volume 4. Morphology D. C. Gans and T. S. Parsons Amphibians. D. H. Taylor and S. I. Guttman (Eds.).

(Eds.). Pp. 285–400. Academic Press, London.

Pp. 185–232. Plenum Press, New York.

Haddad, C. F. B., and Giaretta, A. A. (1999). Visual and acoustic Halliday, T. R., and Heyer, W. R. (1997). The case of the vanish-communication in the Brazilian torrent frog, Hylodes asper ing frogs. MIT's Technology Review May/June: 56–63.

(Anura: Leptodactylidae). Journal of Herpetology 55: Halliday, T. R., and Adler, K. (Eds.) (1986). The Encyclopedia of 324–333.

Reptiles and Amphibians Facts on File Inc., New York.

Haddad, C. F. B., and Prado, C. P. A. (2005). Reproductive Halliday, T. R., and Tejedo, M. (1995). Intrasexual selection and modes in frogs and their unexpected diversity in the Atlantic alternative mating behaviour. In Amphibian Biology. Volume Forest of Brazil. Bioscience 55: 724–724.

2, Social Behaviour. H. Heatwole and B. K. Sullivan (Eds.).

Pp. 419–468. Surrey Beatty & Sons Pty Ltd, Chipping Nor-Goris (Eds.). Pp. 157–167. Herpetological Society of Japan, ton Pty Ltd, N.S.W.

Kyoto.

Halpern, M. (1992). Nasal chemical senses in reptiles: Structure Hayes, M. P. (1983). Predation on the adults and prehatching and function. In Biology of the Reptilia. Volume 18, Physi-stages of glass frogs (Centrolenidae). Biotropica 15: 74–76.

ology. Hormones, Brain, and Behavior. C. Gans and D.

Hayes, T. B. (1997a). Amphibian metamorphosis: An integrative Crews (Eds.). Pp. 422–523. University of Chicago Press, approach. American Zoologist 37: 121–123.

Chicago.

Hayes, T. B. (1997b). Steroids as potential modulators of thyroid Hamilton, J., and Coe, M. (1982). Feeding, digestion and assimila-hormone activity in anuran metamorphosis. American Zoolo-tion of a population of giant tortoises (Geochelone gigantea) gist 37: 185–194.

on Aldabra atoll. Journal of Arid Environments 5: 127–144.

Hayes, T. B., Wu, T. H., and Gill, T. N. (1997). DDT-like effects Handrigan, G. R., Haas, A., and Wassersug, R. J. (2007). Bony-as a result of coricosterone treatment in an anuran amphibian: tailed tadpoles: The development of supernumerary caudal Is DDT a corticoid mimic or a stressor? Environmental Toxi-vertebrae in larval megophryids (Anura). Evolution & Devel-cology and Chemistry 16: 1948–1953.

opment 9: 190–202.

Hays, J., Hoffman, P. D., and Blaustein, A. R. (1995). Differ-Hanken, J. (1986). Developmental evidence for amphibian ori-ences in DNA-repair activity and sensitivity to UV-B light gins. Evolutionary Biology 20: 389–417.

among eggs and oocytes of declining and stable amphibian Hanken, J. (1989). Development and evolution in amphibians.

species. Journal of Cellular Biochemistry 296.

American Scientist 77: 336–343.

Hetherington, T. E. (1985). Role of the opercularis muscle in Hanken, J. and Hall, B. K. (Eds.). (1993). The Skull. Volumes seismic sensitivity in the bullfrog Rana catesbeiana. Journal 1–3. University of Chicago Press, Chicago.

of Experimental Zoology 235: 27–34.

Hardy, D. L. (1994). A reevaluation of suffocation as the cause Heatwole, H. (1999). Sea Snakes. Second Edition. Krieger Publ.

of death during constriction by snakes. Herpetological Co., Malabar, FL.

Review 25: 45–47.

Heatwole, H., and Barthalmus, G. T. (1994). Amphibian Biology.

Harlow, P. S. (2004). Temperature-dependent sex determination Volume 1. The Integument. Surrey Beatty & Sons Pty Ltd, in lizards. In Temperature-Dependent Sex Determination in Chipping Norton Pty Ltd, N.S.W.

Vertebrates. N. Valenzuela and V. Lance (Eds.). Pp. 42–58.

Heatwole, H., and Cogger, H. G. (1993). Family Hydrophiidae.

Smithsonian Books, Washington, D. C.

In Fauna of Australia. Volume 2A. Amphibia & Reptilia. C. J.

Harris, D. J., Marshall, J. C., and Crandall, K. A. (2001). Squa-Gasby, G. J. B. Ross, and P. L. Beesley (Eds.). Pp. 310–318.

mate relationships based on C-mos nuclear DNA sequences: Australian Government Publishing Service, Canberra.

Increased taxon sampling improves bootstrap support.

Heatwole, H., and Guinea, M. L. (1993). Family Laticaudinae.

Amphibia-Reptilia 22: 235–242.

In Fauna of Australia. Volume 2A. Amphibia & Reptilia.

Harshman, J., Huddleston, C. J., Bollback, J. P., Parsons, T. J., C. J. Gasby, G. J. B. Ross, and P. L. Beesley (Eds.).

and Braun, M. J. (2003). True and false gharials: A nuclear Pp. 319–321. Australian Government Publishing Service, gene phylogeny of Crocodylia. Systematic Biology 52: Canberra.

386–402.

Heatwole, H. and Sullivan, B. K. (Eds.) (1995). Amphibian Biol-Hartline, P. H. (1967). The unbelievable fringed turtle. Interna-ogy, Vol. 2, Social Behaviour. Surrey Beaty & Sons, Chip-tional Turtle and Tortoise Society Journal 1: 24–29.

ping Norton, NSW.

Hartmann, M. T., Marques, O. A. V., and Alameida-Santos, Heatwole, H., Firth, B. T., and Stoddart, H. (1975). Influence of S. M. (2005). Reproducive biology of the southern Brazilian season, photoperiod and thermal acclimation on panting pitviiper Bothrops neuwiedi pubescens (Serpentes, Viperi-threshold of Amphibolurus muricatus. Journal of Experimen-dae). Amphibia-Reptilia 25: 77–85.

tal Zoology 191: 183–192.

Hass, C. A., Hoffman, M. A., Densmore, L. D., and Maxson, Heatwole, H., Firth, B. T., and Webb, G. J. W. (1973). Panting L. R. (1992). Crocodilian evolution: Insights from immuno-thresholds of lizards I. some methodological and internal logical data. Molecular Phylogenetics and Evolution 1: influences on panting threshold of an agamid, Amphibolurus 193–201.

muricatus. Comparative Biochemistry and Physiology 46: Hass, C. A., Nussbaum, R. A., and Maxson, L. R. (1993). Immu-799–826.

nological insights into the evolutionary history of caecilian Hedges, S. B. (1986). An electrophoretic analysis of holarctic (Amphibia: Gymnophiona): Relationships of the Seychellean hylid frog evolution. Systematic Zoology 35: 1–21.

caecilians and a preliminary report on family-level relation-Hedges, S. B. (2001b). Afrotheria: Plate tectonics meets geno-ships. Herpetological Mongraphs 7: 56–63.

mics. Proceedings of the National Academy of Sciences Hay, J. M., Ruvinsky, I., Hedges, S. B., and Maxson, L. R.

(USA) 98: 1–2.

(1995). Phylogenetic Relationships of amphibian families Hedges, S. B. (2001a). Molecular evidence for the early history inferred from DNA sequences of mitochondrial 12S and of living vertebrates. Major Events in Early Vertebrate Evo-16S ribosomal RNA genes. Molecular Biology and Evolution lution: Palaeontology, Phylogeny, Genetics and Develop-12: 928–937.

ment 61: 119–134.

Hayashi, T., and Matsui, M. (1989). Preliminary study of phylog-Hedges, S. B. (1996). The origin of West Indian amphibians and eny in the family Salamandridae: allozyme data. In Current reptiles. In Contributions to West Indian Herpetology: A trib-Herpetology in East Asia. M. Matsui, T. Hikida, and R. C.

ute to Albert Schwartz. R. Powell and R. W. Henderson

(Eds.). Pp. 95–128. Society for the Study of Amphibians and Herrel, A., Reilly, S. M., McBrayer, L. D., and Miles, D. B.

Reptiles, Ithaca, NY.

(2007). Herbivory and foraging mode in lizards. In Lizard Hedges, S. B., and Maxson, L. R. (1996). Re: Molecules and Ecology: The Evolutionary Consequences of Foraging Mode.

morphology in amniote phylogeny. Molecular Phylogenetics S. M. Reilly, L. D. McBrayer, and D. B. Miles (Eds.).

and Evolution 6: 312–314.

Pp. 209–236. Cambridge University Press, Cambrdge UK.

Hedges, S. B., and Poling, L. L. (1999). A molecular phylogeny Herrmann, H. -J. (1993). Ruder-und Riedfro¨sche. Baumfro¨sche of reptiles. Science 283: 998–1001.

mit interessantem Verhalten fu¨r attraktive Terriarien. Tetra-Hedges, S. B., Bezy, R. L., and Maxson, L. R. (1991). Phyloge-Verlag, Melle, Germany.

netic relationships and biogeography of xantusiid lizards, Hertz, P. E., Huey, R. B., and Nevo, E. (1982). Fight versus inferred from mitochondrial DNA sequences. Molecular flight: body temperature influences defensive responses of Biology and Evolution 8: 767–780.

lizards. Animal Behaviour 30: 676–679.

Hedges, S. B., Hass, C. A., and Maxson, L. R. (1992). Caribbean Hertz, P. E., Huey, R. B., and Stevenson, R. D. (1993). Evaluat-biogeography: Molecular evidence for dispersal in West ing temperature regulation by field-active ectotherms: The Indian terrestrial vertebrates. Proceedings of the National fallacy of the inappropriate question. American Naturalist Acadademy of Sciences (USA) 89: 1909–1913.

142: 796–818.

Hedges, S. B., Nussbaum, R. A., and Maxson, L. R. (1993). Cae-Hetherington, T. E. (1985). Role of the opercularis muscle in cilian phylogeny and biogeography inferred from mitochon-seismic sensitivity in the bullfrog

Rana catesbeiana. Journal drial DNA sequences of the 12S rRNA and 16S rRNA of Experimental Zoology 235: 27–34.

genes (Amphibia: Gymnophiona). Herpetological Mono-Hetherington, T. E., Jaslow, A. P., and Lombard, R. E. (1986).

graphs 7: 64–76.

Comparative morphology of the amphibian opercularis sys-Heinicke, M. P., Duellman, W. E., and Hedges, S. B. (2007).

tem: I. General design features and functional interpretation.

Major Caribbean and Central American frog faunas origi-Journal of Morphology 190: 43–61.

nated by ancient oceanic dispersal. Proceedings of the Heulin, B. (1990). comparative-study on eggshell membrane of National Academy of Sciences (USA) 104: 10092–10097.

oviparous and parous populations of the lizard Lacerta vivi-Heise, P. J., Maxson, L. R., Dowling, H. G., and Hedges, S. B.

para. Canadian Journal of Zoology 68: 1015–1019.

(1995). Higher-level snake phylogeny inferred from mito-Heyer, W. R. (1967). A herpetofaunal study of an ecological chondrial DNA sequences of 12S rRNA and 16S rRNA transect through the Cordillera de Tilarań, Costa Rica.

genes. Molecular Biology and Evolution 12: 259–265.

Copeia 1967: 259–271.

Hemmer, H. and Alcover, J. A. (Eds.). (1984). Història Biològica Heyer, W. R. (1975). A preliminary analysis of the intergeneric del Ferreret. (Life History of the Mallorcan Midwife Toad).

relationships of the frog family Leptodactylidae. Smithsonian Editorial Moll, Palma de Mallorca.

Contributions to Zoology 199: 1–55.

Henderson, R. W. (1993). Corallus. Catalogue of American Heyer, W. R. (1979). Systematics of the pentadactylus species Amphibians and Reptiles 572: 1–2.

group of the frog genus Leptodactylus (Amphibia: Leptodac-Henderson, R.

W. (2002). Neotropical Treeboas, Natural History tylidae). Smithsonian Contributions from Zoology 301: 1–43.

of the Corallus hortulanus Complex. Kreiger Publishing Heyer, W. R. (1994). Hyla benitezi (Amphibia, Anura, Hylidae) -

Company, Malabar, FL.

first record for Brazil and its biogeographical significance.

Henderson, R. W., and Powell, R. (2007). Biology of the Boas Journal of Herpetology 28: 497–499.

and Pythons. Eagle Mountain Publishing, LC, Eagle Moun-Heyer, W. R., and Crombie, R. I. (2005). Leptodactylus laura-tain, Utah.

miriamae, a distinctive new species of frog (Amphibia: Hennig, W. (1966). Phylogenetic Systematics. University of Chi-Anura: Leptodactylidae) from Rondoˆnia, Brazil. Proceedings cago Press, Chicago.

of the Biological Society of Washington 118: 590–595.

Henrici, A. C. (1994). Tephrodytes brassicarvalis, new genus Heyer, W. R., and Liem, D. S. (1976). Analysis of the interge-and species (Anura: Pelodytidae), from the Arikareean Cab-neric relationships of the Australian frog family Myoba-bage Patch Beds of Montana, USA, and pelodytid-pelobatid trachidae. Smithsonian Contributions from Zoology 233: relationships. Annals of the Carnegie Museum of Natural 1–29.

History 63: 155–183.

Heyer, W. R., and Maxon, L. R. (1982). Distribution, relation-Herbeck, L. A., and Larsen, D. R. (1999). Plethodontid salaman-ships, and zoogeography of lowland frogs. The Leptodactylus der response to silvicultural practices in Missouri Ozark for-complex in South America, with special reference to Amazo-est. Conservation Biology 13: 623–632.

nia. In Biological diversification in the tropics. G. T. Prance Herbst, L. H. (1994). Fibropapillomatosis of marine turtles.

(Ed.). Columbia University Press, New York, NY.

Annual Review of Fish Diseases 4: 389–425.

Heyer, W. R., Donnelly, M. A., McDiarmid, R. W., Hayek, L.-A.

Herbst, L. H., and Klein, P. A. (1995). Green turtle fibropapillo-C., and Foster, M. S. (1994).In Measuring and Monitoring matosis: Challenges to assessing the role of environmental Biological Diversity. Standard Methods for Amphibians cofactors. Environmental Health Perspectives 103, suppl. 4: Smithsonian Institute Press, Washington, D.C.

27–30.

Heyer, W. R., Rand, A. S., Cruz, C. A. G. da, Peixoto, O. L., and Hermann, H. -W., and Joger, U. (1997). Evolution of viperine Nelson, C. E. (1990). Frogs of Boraceía. Arquivos de Zoolo-snakes. In Venomous Snakes, Ecology, Evolution and Snake-gia 31: 231–410.

bite. R. S. Thorpe, W. Wu¨ster, and A. Malhotra (Eds.).

Hille, B. (1992). Ionic Channels of Excitable Membranes Sinauer Pp. 43–61. Zoological Society of London.

Associates, Sunderland, MA.

Hillis, D. M. (1991). The phylogeny of amphibians: Current Internationaux du Centre National de la Recherche Scientifi-knowledge and the role of cytogenetics. In Amphibian Cyto-que 104: 243–279.

genetics and Evolution. D. M. Green and S. K. Sessions Hoffstetter, R., and Gasc, J.-P. (1969). Vertebrae and ribs of (Eds.). Pp. 7–31. Academic Press, San Diego.

modern reptiles. In Biology of the Reptilia. Volume 1.

Hillis, D. M. (2007). Making evolution relevant and exciting to Morphology A, C. Gans, d'A. Bellairs, and T. S. Parsons biology students. Evolution 61: 1261–1264.

(Eds.). Pp. 201–310. Academic Press, London.

Hillis, D. M., and Green, D. M. (1990). Evolutionary changes of Hofman, A., Maxson, L. R., and Arntzen, J. W. (1991). Biochemi-heterogametic sex in the phylogenetic history of amphibians.

cal evidence pertaining to the taxonomic relationships within Journal of Evolutionary Biology. 3: 49–64.

the family Chamaeleonidae. Amphibia-Reptilia 12: 245–265.

Hillis, D. M., and Moritz, C. (1990). An overview of applications Ho¨ggren, M., and Tegelstro¨m, H. (1995). DNA fingerprinting of molecular systematics. In Molecular Systematics, Second shows within-season multiple paternity in the adder (Vipera Edition. D. Hillis and C. Moritz (Eds.). Pp. 502–515. Sinauer berus). Copeia 1995: 271–277.

Associates, Sunderland, Mass.

Holder, M., and Lewis, P. O. (2003). Phylogeny estimation: Tra-Hillis, D. M., and Wilcox, T. P. (2005). Phylogeny of the New ditional and Bayesian approaches. Nature Reviews Genetics World true frogs (Rana). Molecular Phylogenetics and Evo-4: 275–284.

lution 34: 299–314.

Holman, J. A. (1995). Pleistocene Amphibians and Reptiles in Hillis, D. M., Mable, B. K., Larson, A., Davis, S. K., and Zim-North America. Oxford University Press, New York.

mer, E. A. (1996). Nucleic acid IV: Sequencing and cloning.

Holmberg, A. R. (1957). Lizard hunts on the north coast of Peru.

In Molecular Systematics, Second Edition. D. M. Hillis, C.

Fieldiana Anthropology, Chicago Natural History Museum Moritz, and B. K. Mable (Eds.). Pp. 321–381. Sinauer 36: 203–220.

Associates, Inc., Sunderland, Mass.

Holmstrom, W. F. (1978). Preliminary observations on prey Hillis, D. M., Moritz, C., and Mable, B. K. (Eds.) (1996). Molecu-herding in the matamata turtle, Chelus fimbriatus (Reptilia, lar Systematics, Second Edition. Sinauer Associates, Inc., Testudines, Chelidae). Journal of Herpetology 12: 573–674.

Sunderland, Mass.

Honda, M., Ota, H., Kobayashi, Nabhitabhata, J., M., Yong, Hillyard, S. D. (1999). Behavioral, molecular and integrative H.-S., and Hikida, T. (1999). Phylogenetic relationships of mechanisms of amphibian osmoregulation. Journal of Exper-the flying lizards, genus Draco (Reptilia: Agamidae). Zoo-imental

Zoology 283: 662–674.

logical Science 16: 535–549.

Hillyard, S. D., Hoff, K. V., and Propper, C. (1998). The water Honda, M., Ota, H., Kobayashi, Nabhitabhata, J., M., Yong, H. -S., absorption response: A behavioral assay for physiological Sengpku, S., and Hikida, T. (2000). Phylogenetic relationships processes in terrestrial amphibians. Physiological Zoology of the family Agamidae (Reptilia: Iguania) inferred from mito-71: 127–138.

chondrial DNA sequences. Zoological Science 17: 527–537.

Himstedt, W. (1996). Die Blindwu¨hlen. Westarp Wissenschaften, Hoogmoed, M. S. (1969). Notes on the herpetofauna of Surinam.

Magdeburg.

II. On the occurrence of Allophryne ruthveni Gaige Hirayama, R. (1994). Phylogenetic systematics of chelonioid sea (Amphibia, Salientia, Hylidae) in Surinam. Zoologische turtles. The Island Arc 3: 270–284.

Mededelingen 44: 75–81.

Hirayama, R. (1997). Distribution and diversity of Cretaceous che-Hoogmoed, M. S., and Cadle, J. E. (1990). Natural history and lonioids. In Ancient Marine Reptiles. J. M. Callaway and E. L.

distribution of Agalychnis craspedopus (Funkhouser, 1957) Nicholls (Eds.). Pp. 225–241. Academic Press, San Diego.

(Amphibia: Anura: Hylidae). Zoologische Mededelingen 65: Hirayama, R. (1998). Oldest known sea turtle. Nature 392: 129–142.

705–708.

Horne, E. A., and Jaeger, R. G. (1988). Territorial pheromones of Hirshfield, M. F., and Tinkle, D. W. (1975). Natural selection female red-backed salamanders. Ethology 78: 143–152.

and the evolution of reproductive effort. Proceedings of the Hotton, N., MacLean, P. D., Roth, J. J., and Roth, E. C. (1986).

National Academy of Sciences (USA) 72: 2227–2231.

The Ecology and Biology of Mammal-like Reptiles. Smithso-Ho¨dl, W.

(1990). Reproductive diversity in Amazonian lowland nian Institute Press, Washington, D.C.

frogs. Fortschritte der Zoologie 38: 41–60.

Hotton, N., Olson, E. C., and Beerbower, R. (1997). Amniote ori-Hoegg, S., Vences, M., Brinkmann, H., and Meyer, A. (2004).

gins and the discovery of herbivory. In Amniote Origins. Com-Phylogeny and comparative substitution rates of frogs pleting the Transition to Land. S. S. Sumida and K. L. M.

inferred from sequences of three nuclear genes. Molecular Martin (Eds.). Pp. 207–264. Academic Press, San Diego.

Biology and Evolution 21: 1188–1200.

Houck, L. D., and Arnold, S. J. (2003). Courtship and mating Hoff, K. S., and Hillyard, S. D. (1991). Angiotension II stimu-behavior. In Reproductive Biology and Phylogeny of Urodela.

lates cutaneous drinking in the toad, Bufo punctatus: A new D. M. Server (Ed.). Pp. 383–424. Science Publishers, Inc.

perspective on the evolution of thirst in terrestrial vertebrates.

Enfield, NH.

Physiological Zoology 64: 1165–1172.

Houck, L. D., and Sever, D. M. (1994). Role of the skin in reproduc-Hoffstetter, R. (1955). Rhynchocephalia, Squamata. Squamata de tion and behaviour. In Amphibian Biology. Volume 1, The Integ-types modernes. In Traite´ de Paleóntologie. V. J. Piveteau ument. H. Heatwole and G. T. Barthalmus (Eds.). Pp. 351–381.

(Ed.). Pp. 556–605, 606–662, respectively. Masson et Cie, Surrey Beaty & Sons, Chipping Norton Pty Ltd, N.S.W.

E

´ dit, Paris.

Houck, L. D., and Verrell, P. A. (1993). Studies of courtship Hoffstetter, R. (1962). Revue des rećentes acquisitions concer-behavior in plethodontid salamanders: A review. Herpetolo-nant l’historire et la syste´matique des squamates. Colloques gica 40: 175–184.

squamates. Colloques gica 49: 175–184.

Hourdry, J., and Beaumont, A. (1985). Les Me´tamorphoses des sprint performance of geckos maximal at low body tempera-Amphibien. Masson, Paris.

tures? Physiological Zoology 62: 488–504.

Howard, R. D. (1978a). The influence of male-defended oviposi-Huey, R. B., Peterson, C. R., Arnold, S. J., and Porter, W. P.

tion sites on early embryo mortality in bullfrogs. Ecology 59: (1989a). Hot rocks and not-so-hot rocks: Retreat-site selec-789–798.

tion by garter snakes and its thermal consequences. Ecology Howard, R. D. (1978b). The evolution of mating strategies in 70: 931–944.

bullfrogs, Rana catesbeiana. Evolution 32: 850–871.

Huey, R. B., Pianka, E. R., and Schoener, T. W. (Eds.) (1983).

Howard, R. R., and Brodie, E. D., Jr. (1973). A Batesian mimetic Lizard Ecology. Studies of a Model Organism. Harvard Uni-complex in salamanders: Responses of avian predators. Her-versity Press, Cambridge, Mass.

petologica 29: 33–41.

Huey, R. B., Pianka, E. R., Egan, M. E., and Coons, L. W.

Howell, K. M. (2000). An overview of East African amphibian (1974). Ecological shifts in sympatry: Kalahari fossorial studies, past, present and future: A view from Tanzania. Afri-lizards (Typhlosaurus). Ecology 55: 304–316.

can Journal of Herpetology 49: 147–164.

Hughes, G. M. (Ed.) (1976). Respiration of Amphibious Verte-Howes, B. J., Lindsay, B., and Lougheed, S. C. (2006). Range-brates. Academic Press, London.

wide phylogeography of a temperate lizard, the five-lined Humphries, C. J., and Parenti, L. R. (1999). Cladistic Biogeogra-skink (Eumeces fasciatus). Molecular Phylogenetics and phy: Interpreting Patterns of Plant and Animal

Distributions.

Evolution 40: 183–194.

(2nd Edition). Oxford University Press, Oxford.

Howland, J. M. (1992). Life history of Cophosaurus texanus Humphries, R. L. (1956). An unusual aggregation of Plethodon (Sauria: Iguanidae): Environmental correlates and interpopu-glutinosus and remarks on its subspecific status. Copeia lational variation. Copeia 1992: 82–93.

1956: 122–123.

Howland, J. M., Vitt, L. J., and Lopez, P. T. (1990). Life on the Humraskar, D., and Velho, N. (2007). The need for studies on edge: The ecology and life history of the tropidurine iguanid amphibians in India. Current Science 92: 1032.

lizard Uranoscodon superciliosum. Canadian Journal of Hunt, J. A., and Farrar, E. S. (2003). Phenotypic plasticity of the Zoology 68: 1366–1373.

digestive system of tadpoles in response to diet. Integrative Hua, S., and Buffetaut, E. (1997). Part V: Crocodylia. Introduc-and Comparative Biology 43: 934.

tion. In Ancient Marine Reptiles. J. M. Callaway and E. L.

Hunt, R. H., and Ogden, J. J. (1991). Selected aspects of the nest-Nicholls (Eds.). Pp. 357–374. Academic Press, San Diego.

ing ecology of American alligators in Okefenokee Swamp.

Huang, W.-S. (2006). Parental care in the long-tailed skink, Journal of Herpetology 24: 448–453.

Mabuya longicaudata, on a tropical Asian island. Animal Hutchinson, G. E. (1957). Concluding remarks. Cold Spring Har-Behaviour 72: 791–795.

bor Symposia on Quantitative Biology 22: 415–427.

Huang, W.-S. (1997a). Reproductive cycle of the skink, Spheno-Hutchinson, J. H. (1991). Early Kinosterninae (Reptilia: Testu-morphus taiwanensis, in central Taiwan. Journal of Herpe-dines) and their phylogenetic significance. Journal of Verte-tology 31: 287–290.

brate Paleontology 11: 145–167.

Huang, W.-S. (1997b). Reproductive cycle of the oviparous liz-Hutchinson

Huang, W.-S. (1997b). Reproductive cycle of the oviparous liz-Hutchinson, J. H. (1992). Western North American reptile ard Japalura brevipes (Agamidae: Reptilia) in Taiwan, and

amphibian

record

across

the

Eocene/Oligocene

Republic of China. Journal of Herpetology 31: 22–29.

boundary and its climatic implications. In Eocene-Oligocene Huang, W.-S. (1998). Reproductive cycles of the grass lizard, Climatic and Biotic Evolution. D. R. Prothero and W. A. Berg-Takydromus hsuehshanensis, with comments on reproductive gen (Eds.). Pp. 451–463. Princeton University Press, Princeton.

patterns of lizards from the central high elevation area of Tai-Hutchinson, M. N. (1992). Origins of the Australian scincid wan. Copeia 1998: 866–873.

lizards: A preliminary report on the skinks of Riversleigh.

Huey, R. B. (1982). Temperature, physiology, and the ecology of The Beagle 9: 61–70.

reptiles. In Biology of the Reptilia. Volume 12, Physiology C.

Hutchinson, M. N. (1993). Family Scincidae. In Fauna of Aus-Physiological Ecology. C. Gans and F. H. Pough (Eds.).

tralia. Volume 2A. Amphibia & Reptilia. C. J. Gasby, Pp. 25–91. Academic Press, London.

G. J. B. Ross, and P. L. Beesley (Eds.). Pp. 261–279. Austra-Huey, R. B., and Pianka, E. R. (1981a). Ecological consequences lian Government Publishing Service, Canberra.

of foraging mode. Ecology 62: 991–999.

Hutchison, V. H., and Dupre´, R. K. (1992). Thermoregulation.

Huey, R. B., and Pianka, E. R. (1981b). Natural selection for juve-In Environmental Physiology of the Amphibians. M. E. Feder nile lizards mimicking noxious beetles. Science 195: 201–203.

and W. W. Burggren (Eds.). Pp. 206–249. University of Chi-Huey, R. B., and Slatkin, M. (1976). Costs and benefits of lizard cago Press, Chicago.

thermoregulation. The Quarterly Review of Biology 51: Hutchison, V. H., and Larimer, J. (1960). Reflectivity of the inte-363–384.

guments of some lizards from different habitats. Ecology 41: Huey, R. B., and Stevenson, R. D. (1979). Integrating thermal 199–209.

physiology and ecology of ectotherms: A discussion of Hutchison, V. H., Dowling, H. G., and Vinegar, A. (1966). Ther-approaches. American Zoologist 19: 357–366.

moregulation in a brooding female Indian python, Python Huey, R. B., Bennett, A. F., John-Alder, H., and Nagy, K. A.

molurus bivittatus. Science 151: 694–696.

(1984). Locomotor capacity and foraging behaviour of Kala-Hutchison, V. H., Haines, H. B., and Engbretson, G. A. (1976).

hari lacertid lizards. Animal Behaviour 32: 41–50.

Aquatic life at high altitude: Respiratory adaptations in the Huey, R. B., Niewiarowski, P. H., Kaufmann, J., and Herron, Lake Titicaca frog, Telmatobius culeus. Respiration Physiol-J. C. (1989b). Thermal biology of nocturnal ectotherms: Is ogy 27: 115–129.

Hutton, J. M. (1989). Production efficiency at crocodile rearing Irwin, W. P., Amy, J. H., and Lohmann, K. J. (2004). Magnetic stations in Zimbabwe. In Crocodiles. Proceedings of the field distortions produced by protective cages around sea tur-8th Working Meeting of the Crocodile Specialist Group, tle nests: Unintended consequences for orientation and navi-IUCN Pp. 1–15. The World Conservation Union, Gland, gation? Biological Conservation 118: 117–120.

Switzerland.

Iskandar, D. T. (1995). Notes on the second specimen of Bar-Huyghe, K., Vanhooydonck, B., Scheers, H., Molina-Borja, M., bourula kalimantanensis (Amphibia: Anura: Discoglossidae)

(Amphibia: Anura: Discoglossidae).

and Van Damme, R. (2005). Morphology, performance and Raffles Bulletin of Zoology 43: 309–311.

fighting capacity in male lizards, Gallotia galloti. Functional Iverson, J. B. (1978). Impact of feral cats and dogs on popula-Ecology 19: 800–807.

tions

of

West-Indian

rock

iguana,

Cyclura

carinata.

Ineich, I. (1992). La parthenogenese chez les Gekkonidae (Rep-Biological Conservation 14: 63–73.

tilia, Lacertilia): Origine et evolution. Bulletin de la Socie´teÍverson, J. B. (1979). Behavior and ecology of the rock iguana zoologique de France 117: 253–266.

Cyclura carinata. Bulletin of the Florida State Museum, Inger, R. F. (1954). Systematics and zoogeography of Philippine Biological Sciences 24: 175–358.

Amphibia. Fieldiana: Zoology 33: 181–531.

Iverson, J. B. (1982). Adaptations to herbivory in iguanine Inger, R. F. (1966). The systematics and zoogeography of the lizards. In Iguanas of the World: Their Behavior, Ecology, Amphibia of Borneo. Fieldiana: Zoology 52: 1–402.

and Conservation. G. M. Burghardt and A. S. Rand (Eds.).

Inger, R. F. (1967). The development of a phylogeny of frogs.

Pp. 60–67. Noyes Publications, Park Ridge, NJ.

Evolution 21: 369–384.

Iverson, J. B. (1990). Nesting and parental care in the mud turtle, Inger, R. F. (1980). Densities of floor-dwelling frogs and lizards Kinosternon flavescens.

Canadian Journal of Zoology 68: in lowland forests of southeast Asia and Central America.

230–233.

American Naturalist 115: 761–770.

Iverson, J. B. (1991a). Phylogenetic hypotheses for the evolution Inger, R. F. (1986). Diets of tadpoles living in a Bornean rain for-of modern kinosternine turtles. Herpetological Monographs est. Alytes 5: 153–164.

5: 1–27.

Inger, R. F. (1996). Commentary on a proposed classification of Iverson, J. B. (1991b). Life history and demography of the yel-the family Ranidae. Herpetologica 52: 241–246.

low mud turtle, Kinosternon flavescens. Herpetologica 47: Inger, R. F. (1999). Distribution patterns of amphibians in south-373–395.

ern Asia and adjacent islands. In Patterns of Distribution of Iverson, J. B. (1992). A Revised Checklist with Distribution Amphibians. W. E. Duellman (Ed.). Pp. 445–482. Johns Hop-Maps of the Turtles of the World. Privately Printed, Rich-kins University Press, Baltimore, MD.

mond, Ind.

Inger, R. F., and Bacon, J. P. (1968). Annual reproduction and Iverson, J. B. (1998). Molecules, morphology, and mud turtle clutch size in rain forest frogs from Sarawak. Copeia 3: phylogenetics. Chelonian Conservation Biology 3: 113–117.

602–606.

Iverson, J. B., and Mamula, M. R. (1989). Natural growth in Inger, R. F., and Colwell, R. K. (1977). Organization of contigu-the Bahamian iguana Cyclura cychlura. Copeia 1989: ous communities of amphibians and reptiles in Thailand.

502–505.

Ecological Monographs 47: 229–253.

Iverson, J. B., Balgooyen, C. P., Byrd, K. K., and Lyddan, K. K.

Inger, R. F., and Greenberg, B. (1966). Annual reproductive pat-

(1993). Latidtudinal variation in egg and clutch size in terns of lizards from a

Bornean rain forest. Ecology 47: turtles. Canadian Journal of Zoology 71: 2448–2461.

1007–1021.

Iverson, J. B., Higgins, H., Sirulnik, A., and Griffiths, C. (1997).

Inger, R. F., and Lian, T. F. (1996). The Natural History of Local and geographic variation in the reproductive biology of Amphibians and Reptiles in Sabah. Natural History Publica-the snapping turtle (Chelydra serpentina). Herpetologica 53: tions (Borneo) Sdn. Bhd., Kota Kinabalu, Sabah.

96–117.

Inger, R. F., Shaffer, H. B., Koshy, M., and Bakde, R. (1984). A Iwabe, N., Hara, Y., Kumazawa, Y., Shibamoto, K., Saito, Y., report on a collection of amphibians and reptiles from the Miyata, T., and Katoh, K. (2005). Sister group relationship Ponmudi, Kerala, South India. Journal of the Bombay Natu-of turtles to the bird-crocodilian clade revealed by nuclear ral History Society 81: 551–570.

DNA-coded proteins. Molecular Biology and Evolution 22: Inger, R. R., and Stuebing, R. B. (1997). A Field Guide to the 810–813.

Frogs of Borneo. Natural History Publ. (Borneo) Sdn. Bhd., Izecksohn, E. (1993). Treˆs novas espećies de Dendrophryniscus Kota Kinabalu, Sabah.

Jimeńez de la Espada das regioes sudeste e sul do Brasil Iordansky, N. N. (1973). The skull of the Crocodilia. In Biology (Amphibia, Anura, Bufonidae). Revista Brasileira de Zoolo-of the Reptilia. Volume 4. Morphology D. C. Gans and T. S.

gia 10: 473–488.

Parsons (Eds.). Pp. 201–262. Academic Press, London.

Jackman, T. R., Applebaum, G., and Wake, D. B. (1997a). Phy-Irish, F. J., Williams, E. E., and Seling, E. (1988). Scanning elec-logenetic relationships of bolitoglossine salamanders: A tron microscopy of changes in epidermal structure occurring demonstration of the effects of combining morphological during the shedding cycle in squamate reptiles. Journal of and molecular data sets. Molecular Biology and Evolution Morphology 197: 105–126.

14: 883–891.

Irschick, D. J., Vitt, L. J., Zani, P. A., and Losos, J. B. (1997). A Jackman, T. R., Larson, A., de Queiroz, K., and Losos, J. B.

comparison of evolutionary radiations in mainland and (1999). Phylogenetic relationships and tempo of early diver-Caribbean Anolis lizards. Ecology 78: 2191–2203.

sification in Anolis lizards. Systematic Biology 48: 254–285.

Jackman, T., Losos, J. B., Larson, A., and de Queiroz, K.

Janzen, F. J., and Krenz, J. G. (2004). Phylogenetics: Which was (1997b). Phylogenetic studies of convergent adaptive radia-first, TSD or GSD? In Temperature-Dependent Sex Determi-tions in Caribbean Anolis lizards. In Molecular Evolution nation in Vertebrates. N. Valenzuela and V. Lance (Eds.).

and Adaptive Radiation. T. J. Givnish and K. J. Sytsma Pp. 121–130. Smithsonian Books, Washington, D. C.

(Eds.). Pp. 535–557. Cambridge University Press, New York.

Janzen, F. J., and Paukstis, G. (1991). Environmental sex deter-Jackson, C. G., Jr., and Davis, J. D. (1972). Courtship display mination in reptiles: Ecology, evolution, and experimental behavior of Chrysemys concinna suwanniensis. Copeia design. Quarterly Review of Biology 66: 149–179.

1972: 385–387.

Janzen, F. J., and Phillips, P. C. (2006). Exploring the evolution Jacobson, E. R., and Whitford, W. G. (1971). Physiological of environmental sex determination, especially in reptiles.

responses to temperature in the patch-nosed snake Salvadora Journal of Evolutionary Biology 19: 1775–1784.

hexalepis. Herpetologica 27: 289–295.

Janzen, F. J., Krenz, J. G., Haselkorn, T. S., Brodie, E. D. Jr., Jacobson, S. K. (1985). Reproductive behavior and male mating and Brodie, E. D., III. (2002). Molecular phylogeography success in two species of glass frogs (Centrolenidae). Herpe-of common garter snakes (Thamnophis sirtalis) in western tologica 41:

Herpe-of common garter snakes (Thamnophis sirtalis) in western tologica 41: 396–404.

North America: Implications for regional historical forces.

Jaeger, C. B., and Hillman, D. E. (1976). Morphology of gusta-Molecular Ecology 11: 1739–1751.

tory organs. In Frog Neurobiology. A Handbook. R. Llinaś Jenkins, F. A., and Walsh, D. M. (1993). An Early Jurassic cae-and W. Precht (Eds.). Pp. 588–606. Springer-Verlag, Berlin.

cilian with limbs. Nature 365: 246–249.

Jaeger, R. G. (1976). A possible prey-call window in anuran Jennings, M. R., and Hayes, M. P. (1985). Pre-1900 overharvest auditory perception. Copeia 1976: 833–834.

of California red-legged frogs (Rana aurora draytonii): The Jaeger, R. G. (1981). Dear enemy recognition and the costs of inducement for bullfrog (Rana catesbeiana) introduction.

aggression between salamanders. American Naturalist 117: Herpetologica 41: 94–103.

962–974.

Jennings, W. B., and Pianka, E. R. (2004). Tempo and timing of Jaeger, R. G. (1986). Pheromonal markers as territorial advertise-the Australian Varanus radiation. In Varanoid Lizards of the ment by terrestrial salamanders. In Chemical Signals in Ver-World. E. R. Pianka and D. R. King (Eds.). Indiana Univer-tebrates 4. D. Duvall, D. Mu¨ller-Schwarze, and R. M.

sity Press, Bloomington, IN.

Silverstein (Eds.). Pp. 191–203. Plenum Press, New York.

Jennings, W. B., Pianka, E. R., and Donnellan, S. (2003). Sys-Jaeger, R. G., and Forester, D. C. (1993). Social behavior of tematics of lizards in the family Pygopodidae with implica-plethodontid salamanders. Herpetologica 49: 163–175.

tions for the diversification of Australian temperate biotas.

Jaeger, R. G., Goy, J., Tarver, M., and Marquez, C. (1986). Sal-Systematic Biology 52: 757–780.

amander territoriality: Pheromonal markers as advertisement Jenssen, T. A. (1970a). The ethoecology of Anolis nebulosus by males. Animal Behaviour 34: 860–864.

(Sauria: Iguanidae). Journal of Herpetology 4: 1–38.

Jaeger, R. G., Kalvarsky, D., and Shimizu, N. (1982). Territorial Jenssen, T. A. (1970b). Female response to filmed displays of behaviour of the red-backed salamander: Expulsion of intru-Anolis nebulosus (Sauria, Iguanidae). Animal Behaviour 18: ders. Animal Behaviour 30: 490–496.

640–647.

Jaffe, M. (1994). and No Birds Sing. The Story of an Ecological Jenssen, T. A., and Hover, E. L. (1976). Display analysis of the Disaster in a Tropical Paradise. Simon & Schuster, New signature display of Anolis limifrons (Sauria: Iguanidae).

York.

Behaviour 57: 227–240.

Jaksıć, F. M., and Schwenk, K. (1983). Natural history observa-Jenssen, T. A., and Nunez, S. C. (1998). Spatial and breeding tions on Liolaemus magellanicus, the southernmost lizard in relationships of the lizard Anolis carolinensis: Evidence of the world. Herpetologica 39: 457–461.

intrasexual selection. Behaviour 135: 981–1003.

James, C. D. (1991). Annual variation in reproductive cycles of Jenssen, T. A., Decourcy, K. R., and Congdon, J. D. (2005).

scincid lizards (Ctenotus) in central Australia. Copeia 1991: Assessment in contests of male lizards (Anolis carolinensis): 744–760.

How should smaller males respond when size matters? Ani-James, C. D., and Shine, R. (1985). The seasonal timing of repro-mal Behaviour 69: 1325–1336.

duction: A tropical-temperate comparison in Australian Jiang, J. P., and Zhou, K. Y. (2005). Phylogenetic relationships lizards. Oecologia 67: 464–474.

among Chinese ranids inferred from sequence data set of James, C. D., and Shine, R. (1988). Life-history strategies of 12S and 16S rDNA. Herpetological Journal 15: 1–8.

Australian lizards: A comparison between the tropics and Joanen, T. (1969). Nesting ecology of alligators in Louisiana.

the temperate zone. Oecologia 75: 307–316.

Proceedings of the Annual Conference of the Southeastern James, F. C., and McCullough, C. E. (1985). Data analysis and Association

of

Game

and

Fish

Commissioners

23:

the design of experiments in ornithology. In Current Orni-141–151.

thology. Vol. 2. R. F. Johnston (Ed.). Pp. 1–63.

Joanen, T., and McNease, L. (1980). Reproductive biology of the James, F. C., and McCullough, C. E. (1990). Multivariate analy-American alligator in soutwest Lousiana. In Reproductive sis in ecology and systematics: Panacea or Pandora's box?

Biology and Disease of Captive Reptiles. J. B. Murphy and Annual Review of Ecology and Systematics 21: 129–166.

J. T. Collins (Eds.). Pp. 153–159. Society for the Study of Jameson, D. L. (1955). The population dynamics of the cliff frog, Amphibians and Reptiles, Athens, Ohio.

Syrrhophus marnocki. American Midland Naturalist 54: Joger, U. (1991). A molecular phylogeny of agamid lizards.

342–381.

Copeia 1991: 616–622.

Joglar, R. L., and Burrowes, P. A. (1996). Declining amphibian Junqueira, L. C. U., Jared, C., and Antoniazzi, M. M. (1999).

populations in Puerto Rico. In Contribution to West Indian Structure of the caecilian Siphonops annulatus (Amphibia, Herpetology. A Tribute to Albert Schwartz. R. Powell and Gymnophiona): General aspect of the body, disposition of R. W. Henderson (Eds.). Pp. 371–380. Society for the Study the organs and structure of the mouth, oesophagus and stom-of Amphibians and Reptiles, Ithaca, NY.

ach. Acta Zoologica 80: 75–84.

Joglar, R. L., Burrowes, P. A., and Rios, N. (1996). Biology Justus, J. T., Sandomir, M., Urquhart, T., and Ewan, B. O.

of the Purto Rican cave-dwelling frog, Eleutherodactylus (1977). Developmental rates of two species of toads from cooki,

and

some

recommendations

for

conservation.

the desert Southwest. Copeia 1977: 592–594.

In Contribution to West Indian Herpetology. A Tribute to Kachigan, S. K. (1982). Multivariate Statistical Analysis. A Con-Albert Schwartz. R. Powell and R. W. Henderson (Eds.).

ceptual Introduction. Radius Press, New York.

Pp. 251–258. Society for the Study of Amphibians and Rep-Kalb, H. J., and Zug, G. R. (1990). Age estimates for a popula-tiles, Ithaca, NY.

tion of American toads, Bufo americanus (Salientia: Bufoni-Johnson, C. R. (1969). Aggregation as a means of water conser-dae), in northern Virginia. Brimleyana 16: 79–86.

vation in juvenile Limnodynastes from Australia. Herpetolo-Kaminsky, S. D., Linsenmair, K. E., and Grafe, T. U. (1999).

gica 25: 275–276.

Reproductive timing, nest construction and tadpole guidance Johnson, S. A. (2003). Orientation and migration distances of a in the African pig-nosed frog, Hemisus marmoratus. Journal pond-breeding salamander (Salamandridae, Notophthalmus of Herpetology 33: 119–123.

perstriatus). Alytes 21: 3–22.

Kardong, K. V. (1992). Proximate factors affecting guidance of Johnston, G. R., and Richards, S. J. (1993). Observations on the the rattlesnake strike. Zoologische Jahrbuecher Abteilung breeding biology of a microhylid frog (genus Oreophryne) fuer Anatomie und Ontogenie der Tiere 122: 233–244.

from New Guinea. Transactions of the Royal Society of South Kardong, K. V. (1995). Vertebrates: Comparative Anatomy, Australia 117: 105–107.

Function, Evolution. William C. Brown Publishers, Dubu-Joly, J. (1968). Donneés ećologiques sur la salamandre tacheteé que, IA.

Salamandra Salamandra.

Annalles

Sciences

Naturelles

Kardong, K. V. (1997). Squamates at geological boundaries: Zoologiques 12: 301–366.

Unbounded evolution. Zoology 100: 152–163.

Jones, D. R. (1996). The crocodilian central circulation: Reptilian Kardong, K. V. (1998). Vertebrates. Comparative Anatomy, or avian? Verhandlungen der Deutschen Zoologischen Gesell-Function, Evolution. Second Edition. McGraw-Hill, New schaft 89: 209–218.

York.

Jones, T. R., Kluge, A. G., and Wolf, A. J. (1993). When theories Kardong, K. V. (2006). Vertebrates. Comparative Anatomy, and methodology clash: A phylogenetic reanalysis of the Function, Evolution. Fourth Edition. McGraw Hill, Boston, North

American

ambystomatid

salamanders

(Caudata:

MA.

Ambystomatidae). Systematic Biology 42: 92–102.

Kardong, K. V., and Bels, V. L. (1998). Rattlesnake strike behav-Jorgensen, C. B. (1992). Growth and reproduction. In Environ-ior: Kinematics. Journal of Experimental Biology 201: mental Physiology of the Amphibians. M. E. Feder and 837–850.

W. W. Burggren (Eds.). Pp. 439–466. University of Chicago Kareiva, P. (2008). Ominous trends in nature recreation. Pro-Press, Chicago.

ceedings of the National Academy of Sciences (USA) 105: Jorgensen, C. B. (1997). 200 years of amphibian water economy: 2757–2758.

From Robert Townson to the present. Biological Reviews of Karraker, N. E., Pilliod, D. S., Adams, M. J., Bull, E. L., Corn, the Cambridge Philosophical Society 72: 153–237.

P. S., Diller, L. V., Dupuis, L. A., Hayes, M. P., Hossack, Joyce, W. G., Parham, J. F., and Gauthier, J. A. (2004). Develop-B. R., Hodgson, G. R., Hyde, E. J., Lohman, K., Norman, ing a protocol for the conversion of rank-based taxon names B. R., Ollivier, L. M., Pearl, C. A., and Peterson, C. R.

to phylogenetically defined clade names, as exemplified by (2006). Taxonomic variation in oviposition by tailed frogs turtles. Journal of Paleontology 78: 989–1013.

(Ascaphus spp.). Northwestern Naturalist 87: 87–97.

Junca´, F. A. (1998). Reproductive biology of Colostethus ste-Kats, L. B., Petranka, J. W., and Sih, A. (1988). Antipredator pheni and Colostethus marchesianus (Dendrobatidae), with defenses and the persistence of amphibian larvae with fishes.

the description of a new anuran mating behavior. Herpetolo-Ecology 69: 1865–1870.

gica 54: 377–387.

Katz, U. (1989). Strategies of adaptation to osmotic stress in Junca´, F. A., Altig, R., and Gascon, C. (1994). Breeding biology anuran Amphibia under salt and burrowing conditions. Com-of Colostethus stepheni, a dendrobatid frog with a nontran-parative Biochemistry and Physiology 93A: 499–503.

sported nidicolous tadpole. Copeia 3: 747–750.

Kearney, M. (2003a). Diet in the amphisbaenian Bipes biporus.

Jungfer, K.-H. (1996). Reproduction and parental care of the Journal of Herpetology 37: 404–408.

coronated treefrog, Anotheca spinosa (Steindachner, 1864) Kearney, M. (2003b). Systematics and evolution of the Amphis-

(Anura: Hylidae). Herpetologica 52: 25–32.

baenia: A phylogenetic hypothesis based on morphological Jungfer, K.-H., and Schiesari, L. C. (1995). Description of a central evidence from fossil and recent forms. Herpetological Mono-Amazonian and Guianan tree frog, genus Osteocephalus graphs 17: 1–75.

(Anura, Hylidae), with oophagous tadpoles. Alytes 13: 1–13.

Kearney, M., and Shine, R. (2004). Developmental success, sta-Jungfer, K.-H., and Weygoldt, P. (1999). Biparental care in the bility, and plasticity in closely related parthenogenetic and tadpole-feeding Amazonian treefrog Osteocephalus oopha-sexual lizards (Heteronotia, Gekkonidae). Evolution 58: gus. Amphibia-Reptilia 20: 235–249.

1560–1572.

Kearney, M., and Stuart, B. L. (2004). Repeated evolution of building gladiator frog. Miscellaneous Publications, Museum limblessness and digging heads in worm lizards revealed by of Zoology, University of Michigan 160: 1–170.

DNA from old bones. Proceedings of the Royal Society of Kluge, A. G. (1987). Cladistic relationships among the Gekko-London Series B-Biological

Sciences 271: 1677–1683.

noidea (Squamata, Sauria). Miscellaneous Publications, Kearney, M., Blacket, M. J., Strasburg, J. L., and Moritz, C.

Museum of Zoology, University of Michigan 173: 1–54.

(2006). Waves of parthenogenesis in the desert: Evidence Kluge, A. G. (1989). Progess in squamate classification. Herpe-for the parallel loss of sex in a grasshopper and a gecko from tologica 45: 368–379.

Australia. Molecular Ecology 15: 1743–1748.

Kluge, A. G. (1991a). Checklist of gekkonoid lizards. Smithso-Kelly, C. M. R., Barker, N. P., and Villet, M. H. (2003). Phylo-nian Herpetological Information Service 85: 1–35.

genetics of advanced snakes (Caenophidia) based on four Kluge, A. G. (1991b). Boine snake phylogeny and research mitochondrial genes. Systematic Biology 52: 439–459.

cycles. Miscellaneous Publications, Museum of Zoology, Kennett, R., Christian, K., and Pritchard, D. (1993a). Underwater University of Michigan 178: 1–58.

nesting of the tropical freshwater turtle, Chelodina rugosa.

Kluge, A. G. (1993a). Aspidites and the phylogeny of pythonine Australian Journal of Zoology 41: 47–52.

snakes. Records of the Australian Museum, supplement 19: Kennett, R., Georges, A., and Palmer-Allen, M. (1993b). Early 1–77.

develomental arrest during immersion of eggs of a tropical Kluge, A. G. (1993b). Calabaria and the phylogeny of erycine freshwater turtle, Chelodina rugosa (Testudinata: Chelidae), snakes. Zoological Journal of the Linnean Society 107: from northern Australia. Australian Journal of Zoology 41: 293–351.

37–45.

Kluge, A. G., and Farris, J. S. (1969). Quantitative phyletics and Keogh, J. S. (1998). Molecular phylogeny of elapid snakes and a the evolution of anurans. Systematic Zoology 18: 1–32.

consideration of their biogeographic history. Biological Jour-Knapp, R. A., and Morgan, J. A. T. (2006). Tadpole mouthpart nal of the Linnean Society 63: 177–203.

depigmentation as an accurate indicator of chytridiomycosis, Kiester, A. R., Gorman, G. C., and Arroyo, D. C. (1975). Habitat an emerging disease of amphibians. Copeia 2006: 188–197.

selection behavior of three species of Anolis lizards. Ecology Knowles, R., Mahony, M., Armstrong, J., and Donnellan, S.

56: 220–225.

(2004). Systematics of sphagnum frogs of the genus Philoria King, D., and Green, B. (1993). Goanna. The Biology of Varanid (Anura: Myobatrachidae) in eastern Australia, with the Lizards. New S. Wales University Press, Kensington, N.S.W.

description of two new species. Records of the Australian King, M., and Horner, P. (1993). Family Gekkonidae. In Fauna Museum 56: 57–74.

of Australia. Volume 2A. Amphibia & Reptilia. C. J. Gasby, Kobel, H. R., Loumont, C., and Tinsley, R. C. (1996). The extant G. J. B. Ross, and P. L. Beesley (Eds.). Pp. 221–233. Austra-species. In The Biology of Xenopus. R. C. Tinsley and H. R.

lian Government Publishing Service, Canberra.

Kobel (Eds.). Pp. 9–33. Zoological Society of London, Kinkead, R. (1997). Episodic breathing in frogs: Converging London.

hypotheses on neural control of respiration in air breathing Kochva, E. (1978). Phylogeny of oral glands in reptiles as related vertebrates. American Zoologist 37: 31–40.

to the origin and evolution of snakes. In Toxins: Animal, Kitimasak, W., Thirakhupt, K., and Moll, D. L. (2003). Eggshell Plant and Microbial. P. Rosenberg (Ed.). Pp. 29–37. Perga-structure of the Siamese narrow-headed softshell turtle mon Press, Oxford.

Chitra chitra Nupthand, 1986 (Testudines: Trionychidae).

Kofron, C. P. (1983). Female reproductive cycle of the Neotrop-ScienceAsia 29: 95–98.

ical snail-eating snake Sibon sanniola in northern Yucatan, Kizirian, D. A.

(1996). A review of Ecuadorian Proctoporus Mexico. Copeia 1983: 963–969.

(Squamata: Gymnophthlamidae) with descriptions of nine Kofron, C. P. (1988). The Central and South American new species. Herpetological Monographs 10: 85–155.

blindsnakes of the genus Anomalepis. Amphibia-Reptilia 9: Klauber, L. M. (1982). Rattlesnakes. Their Habits, Life Histories, 7–14.

and Influence on Mankind. Abridged Edition. University of Ko¨hler, J., Glaw, F., and Vences, M. (1997). Notes on the repro-California Press, Berkeley.

duction of Rhombophryne (Anura: Microhylidae) at Nosy Be, Klaver, C. J. J., and Bo¨hme, W. (1986). Phylogeny and classifi-northen Madagascar. Revue francaise de Aquariologie (Hercation of the Chamaeleonidae (Sauria) with special reference petologie) 24: 1–2.

to hemipenis morphology. Bonner Zoologische Monogra-Kok, D., du Preez, L. H., and Channing, A. (1989). Channel con-phien 22: 1–64.

struction by the African bullfrog: Another anuran parental Klaver, C. J. J., and Bo¨hme, W. (1997). Chamaeleonidae. Das care strategy. Journal of Herpetology 23: 435–437.

Tierreich 109: 1–306.

Kokubum, M. N. D., and Giaretta, A. A. (2005). Reproductive Kluge, A. G. (1974). A taxonomic revision of the lizard family ecology and behaviour of a species of Adenomera (Anura, Pygopodidae. Miscellaneous Publications, Museum of Zool-Leptodactylinae) with endotrophic tadpoles: Systematic ogy, University of Michigan 147: 1–221.

implications. Journal of Natural History 39: 1745–1758.

Kluge, A. G. (1976). Phylogenetic relationships in the lizard Komnick, H. (1986). Chloride cells and salt glands. In Biology of family Pygopodidae: An evaluation of theory, methods and the Integument. G. Matoltsy and K. S. Richards (Eds.).

data. Miscellaneous Publications, Museum of Zoology, Uni-Pp. 499–516. Springer Verlag, Berlin.

versity of Michigan 152: 1–72.

Kozak, K. H., Blaine, R. A., and Larson, A. (2006). Gene Kluge, A. G.

(1981). The life history, social organization, and lineages and eastern North American palaeodrainage basins: parental behavior of Hyla rosenbergi Boulenger, a nest-phylogeography and speciation in salamanders of the

Eurycea bislineata species complex. Molecular Ecology 15: sequence analysis of the African Gerrhosauridae. Biological 191–207.

Journal of the Linnean Society 78: 253–261.

Kraus, F., and Brown, W. M. (1998). Phylogenetic relationships Lambiris, A. J. L. (1989). The frogs of Zimbabwe. Museo Regio-of colubroid snakes based on mitochondrial DNA sequences.

nale di Scienze Naturali Monographia 10: 1–247.

Zoological Journal of the Linnean Society 122: 455–487.

Lamotte, M., and Ohler, A. (2000). Revision of the Ptychadena Kraus, F., and Campbell, E. W. (2002). Human-mediated escala-stenocephala species group (Amphibia, Anura). Zoosystema tion of a formerly eradicable problem: The invasion of Carib-22: 569–583.

bean frogs in the Hawaiian Islands. Biological Invasions 4: Lampo, M., and De Leo, G. A. (1998). The invasion ecology of 327–332.

the toad Bufo marinus: From South America to Australia.

Kraus, F., Campbell, E. W., Allison, A., and Pratt, T. (1999). A Ecological Applications 8: 388–396.

Field Guide to Florida Reptiles and Amphibians. Gulf Pub-Lancaster, J. R., Wilson, P., and Espinoza, R. E. (2006). Physio-lishing Company, Houston, TX.

logical benefits as precursors of sociality: Why banded Krishna, S. N., and Krishna, S. B. (2006). Visual and acoustic geckos band. Animal Behaviour 72: 199–207.

communication in an endemic stream frog, Micrixalus saxi-Lance, V. A., Elsey, R. M., and Lang, J. W. (2000). Sex ratios of colus in the Western Ghats, India. Amphibia-Reptilia 27: American alligators (Crocodylidae): Male or female biased?

143–147.

143–147.

Journal of Zoology, London 252: 71–78.

Kronauer, D. J. C., Bergmann, P. J., Mercer, J. M., and Russell, Lancini, A. R., and Kornacker, P. M. (1989). Die Schlangen von A. P. (2005). A phylogeographically distinct and deep diver-Venezuela. Verlag Armitano Ed. C. A, Carcas.

gence in the widespread Neotropical turnip-tailed gecko, Lande, R. (1980). Sexual dimorphism, sexual selection, and Thecadactylus rapicauda. Molecular Phylogenetics and Evo-adaptation in polygenic characters. Evolution 34: 292–305.

lution 34: 431–437.

Landmann, L. (1975). The sense organs in the skin of the head Kropach, C. (1971). Sea snake (Pelamis platurus) aggregations of Squamata (Reptilia). Israel Journal of Zoology 24: on slicks in Panama. Herpetologica 27: 131–135.

99–135.

Kru¨gel, P., and Richter, S. (1995). Syncope antenori—a brome-Landmann, L. (1986). Epidermis and dermis. In Biology of the liad breeding frog with free-swimming, nonfeeding tadpoles Integument. J. Vertebrates, A. G. Bereiter-Hahn, K. S.

(Anura, Microhylidae). Copeia 1995: 955–963.

Matoltsy, and Richards (Eds.). Pp. 150–187. Springer Verlag, Kuchling, G. (1998). Managing the last survivors: Integration of Berlin.

in situ and ex situ conservation of Pseudemydura umbrina.

Lang, J. W. (1989). Social behavior. In Crocodiles and Alligator.

In Proceedings: Conservation, Restoration, and Management C. A. Ross (Ed.). Pp. 102–117. Golden Press Pty Ltd, Silver-of Tortoises and Turtles – An International Conference water, N.S.W.

[1997]. J. V. Abbema (Ed.). Pp. 339–344. New York Turtle Lang, J. W., and Andrews, H. V. (1994). Temperature-dependent and Tortoise Society, New York.

sex determination in crocodilians. Journal of Experimental Kuchling, G. (1999). The Reproductive Biology of the Chelonia.

Zoology 270: 28–44.

Springer-Verlag, Berlin.

Lang, M. (1989a). Phylogenetic and biogeographic patterns of Kunte, K. (2004). Natural history and reproductive behavior of basiliscine iguanians (Reptilia: Squamata: "Iguanidae"). Bon-Nyctibatrachus cf. humayuni (Anura: Ranidae). Herpetologi-ner Zoologische Monographien 28: 1–172.

cal Review 35: 137–140.

Lang, M. (1989b). Notes on the genus Bombina Oken (Anura: Kupfer, A., Muller, H., Antoniazzi, M. M., Jared, C., Greven, H., Bombinatoridae): III. Anatomy, systematics, hybrization, Nussbaum, R. A., and Wilkinson, M. (2006). Parental invest-fossil record and biogeography. British Herpetological Soci-ment by skin feeding in a caecilian amphibian. Nature 440: ety Bulletin 28: 43–49.

926–929.

Lang, M. (1991). Generic relationships within Cordyliformes Kupfer, A., Nabhitabhata, J., and Himstedt, W. (2005). Life his-

(Reptilia: Squamata). Bulletin de l'Institut Royal des tory of amphibians in the seasonal tropics: Habitat, commu-Sciences Naturelles de Belgique 61: 121–188.

nity

and

population

ecology

of

a

caecilian

(genus

Lannoo, M. J. (1987a). Neuromast topography in anuran amphi-Ichthyophis). Journal of Zoology, London 266: 237–247.

bians. Journal of Morphology 191: 115–129.

Kusano, T. (1980). Breeding and egg survival of a population of Lannoo, M.

Kusano, T. (1980). Breeding and egg survival of a population of Lannoo, M. J. (1987b). Neuromast topography in urodele amphi-a salamander,

Hynobius

nebulosus

tokyoensis

Tago.

bians. Journal of Morphology 191: 247–263.

Researches on Population Ecology 21: 181–196.

Lanza, B., Caputo, V., Nascetti, G., and Bullini, L. (1995). Mor-Kuzmin, S. L. (1995). The Clawed Salamanders of Asia. Westarp phologic and genetic studies of the European plethodontid Wissenschaften, Magdeburg.

salamanders: taxonomic inferences (genus Hydromantes).

Lailvaux, S. P., and Irschick, D. J. (2006). No evidence for Museo Regionale di Scienza Naturali (Torino) Monographias female association with high-performance males in the green 14: 1–366.

anole lizard, Anolis carolinensis. Ethology 112: 707–715.

Lappin, A. K., and Husak, J. F. (2005). Weapon performance, not Lailvaux, S. P., and Irschick, D. J. (2007). The evolution of per-size, determines mating success and potential reproductive formance-based male fighting ability in Caribbean Anolis output in the collared lizard (Crotaphytus collaris). American lizards. American Naturalist 170: 573–586.

Naturalist 166: 426–436.

Lamb, T., Meeker, A. M., Bauer, A. M., and Branch, W. R.

Largen, M. J. (1991). A new genus and species of petropedetine (2003). On the systematic status of the desert plated lizard frog (Amphibia Anura Ranidae) from high altitude in the (Angolosaurus skoogi): Phylogenetic inference from DNA mountains of Ethiopia. Tropical Zoology 4: 139–152.

Larson, A. (1991). A molecular perspective on the evolutionary threatened

Larson, A. (1991). A molecular perspective on the evolutionary threatened California red-legged frog. Conservation Biology relationships of the salamander families. Evolutionary Biol-13: 613–622.

ogy 25: 211–277.

Lawson, R., Slowinski, J. B., and Burbrink, F. T. (2004). A Larson, A., and Dimmick, W. W. (1993). Phylogenetic relation-molecular approach to discerning the phylogenetic placement ships of the salamander families: An analysis of congruence of the enigmatic snake Xenophidion schaeferi among the among morphological and molecular characters. Herpetolog-Alethinophidia. Journal of Zoology, London 263: 285–294.

ical Monographs 7: 77–93.

Lawson, R., Slowinski, J. B., Crother, B. I., and Burbrink, F. T.

Larson, A., Weisrock, D. W., and Kozak, K. H. (2003). Phyloge-

(2005). Phylogeny of the Colubroidea (Serpentes): New evi-netic systematics of salamanders (Amphibia: Urodela), a dence from mitochondrial and nuclear genes. Molecular Phy-review. In Reproductive Biology and Phylogeny of Urodela logenetics and Evolution 37: 581–601.

(Amphibia). D. M. Sever (Ed.). Pp. 31–108. Science Publish-Leache, A. D., and McGuire, J. A. (2006). Phylogenetic relation-ers, Inc. Enfield, New Hampshire.

ships of horned lizards (Phrynosoma) based on nuclear and Larson, J. H., and Guthrie, D. J. (1985). The feeding system of mitochondrial data: Evidence for a misleading mitochondrial terrestrial tiger salamanders (Ambystoma tigrinum melanos-gene tree. Molecular Phylogenetics and Evolution 39: tictum Baird). Journal of Morphology 147: 137–154.

628–644.

Lasiewski, R. C., and Bartholomew, G. A. (1969). Condensation Leary, C. J., Fox, D. J., Shepard, D. B., and Garcia, A. M.

as a mechanism for water gain in nocturnal desert poiki-

(2005). Body size, age, growth and alternative mating tactics lotherms. Copeia 1969: 405–407.

in toads: Satellite males are smaller but not younger than Lathrop, A. (1997). Taxonomic review of the megophryid frogs calling males. Animal Behaviour 70:

Taxonomic review of the megophryid frogs calling males. Animal Behaviour 76: 663–671.

(Anura: Pelobatoidea). Asiatic Herpetological Research 7: Leary, C. J., Garcia, A. M., and Knapp, R. (2006). Elevated cor-68–79.

ticosterone levels elicit non-calling mating tactics in male Lauder, G., and Gillis, G. B. (1997). Origin of the amniote feed-toads independently of changes in circulating androgens.

ing mechanism: Experimental analyses of outgroup clades.

Hormones and Behavior 49: 425–432.

In Amniote Origins. Completing the Transition to Land.

Leary, C. J., Jessop, T. S., Garcia, A. M., and Knapp, R. (2004).

S. S. Sumida and K. L. M. Martin (Eds.). Pp. 169–206. Aca-Steroid hormone profiles and relative body condition of call-demic Press, San Diego.

ing and satellite toads: implications for proximate regulation Laurance, W. F. (1996). Catastrophic declines of Australian rain-of behavior in anurans. Behavioral Ecology 15: 313–320.

forest frogs: Is unusual weather responsible? Biological Con-Lebedev, O. A. (1997). Palaeontology: Fins made for walking.

servation 77: 203–212.

Nature 390: 21–22.

Laurance, W. F., McDonald, K. R., and Speare, R. (1996). Epi-Lee, J. C. (1975). The autecology of Xantusia henshawi hen-demic disease and the catastrophic decline of Australian rain-shawi (Sauria: Xantusiidae). Transactions of the San Diego forest frogs. Conservation Biology 10: 406–413.

Soceity of Natural History 17: 259–278.

Laurent, R. F. (1954). Aperc¸u de la biogeógraphie des batraciens Lee, J. C. (1996). The Amphibians and Reptiles of the Yucatań et des reptiles de la re´gion des grands lacs. Bulletin de la Peninsula. Comstock Publishing Associates, Ithaca, N.Y.

Socie´teŹoologique de France 79: 290–310.

Lee, M. S. Y. (1993). The origin of the turtle body plan: Bridging Laurent, R. F. (1979). Herpetofaunal relationships between a famous morphological gap

R. F. (1979). Herpetofaunal relationships between a famous morphological gap. Science 261: 1716–1720.

Africa and South America. In The South American Herpeto-Lee, M. S. Y. (1995). Historical burden in systematics and the fauna: Its Origin, Dispersal, and Evolution. W. E. Duellman interrelationships of ’parareptiles. Biological Reviews 70: (Ed.). Pp. 55–71. Museum of Natural History, University of 459–547.

Kansas, Monograph No. 7, Lawrence, KS.

Lee, M. S. Y. (1997). Pareisaur phylogeny and the origin of Laurent, R. F., and Teran, E. M. (1981). Lista de los anfibios y turtles. Zoological Journal of the Linnean Society 120: reptiles de la provincia de Tucumań. Miscelanea de la Fun-197–280.

dacioń Miguel Lillo 71: 1–15.

Lee, M. S. Y. (1997). The phylogeny of varanoid lizards and Laurin, M. (2002). Tetrapod phylogeny, amphibian origins, and the affinities of snakes. Philosophical Transactions of the the definition of the name tetrapoda. Systematic Biology 51: Royal Society of London Series B-Biological Sciences 352: 364–369.

53–91.

Laurin, M., and Reisz, R. R. (1995). A reevaluation of early Lee, M. S. Y. (1998). Convergent evolution and character corre-amniote phylogeny. Zoological Journal of the Linnean lation in burrowing reptiles: Towards a resolution of squa-Society 113: 165–223.

mate relationships. Biological Journal of the Linnean Laurin, M., and Reisz, R. R. (1997). A new perspective on tetra-Society 65: 369–453.

pod phylogeny. In Amniote Origins. Completing the Transi-Lee, M. S. Y. (2005). Squamate phylogeny, taxon sampling, and tion to Land. S. S. Sumida and K. L. M. Martin (Eds.).

data congruence. Organisms, Diversity & Evolution 5: Pp. 9–59. Academic Press, San Diego.

25–45.

Lawler, S. P. (1989). Behavioural responses to predators and pre-Lee, M. S. Y., and Scanlon, J. D. (2002). Snake phylogeny based dation risk in four species of larval anurans. Animal Beha-on osteology, soft anatomy and ecology. Biological Review viour 38: 1039–1047.

77: 333–401.

Lawler, S. P., Dritz, D., Strange, T., and Holyoak, M. (1999).

Lee, M. S. Y., Scanlon, J. D., and Caldwell, M. W. (2000). Snake Effects of introduced mosquitofish and bullfrogs on the origins. Science 288: 1343–1344.

Legler, J. M., and Fitch, H. S. (1957). Observations on hiberna-Lescure, J. (1979). E

´ tude taxonomique et ećo-e´thologique d’un tion and nests of the collared lizard, Crotaphytus collaris.

ampihibien des petites Antilles Leptodactylus fallax Muller, Copeia 1957: 305–307.

1926 (Leptodactylidae). Bulletin du Museúm National d’His-Legler, J. M., and Georges, A. (1993). Family Chelidae. In Fauna toire Naturelle, Paris 1: 757–774.

of Australia. Volume 2A, Amphibia & Reptilia. C. J. Glasby, Lescure, J. (1986a). La vie sociale de l’adulte. In Traite´ de Zool-G. J. B. Ross, and P. I. Beesley (Eds.). Pp. 120–128. Australian ogie. Anatomie, Syste´matique, Biologie. Tome XIV. Batra-Government Public Service, Canberra.

ciens. P.-P. Grasseánd M. Delsol (Eds.). Pp. 525–537.

Lehtinen, R. M., and Skinner, A. A. (2006). The enigmatic Masson, Paris.

decline of Blanchard’s Cricket Frog (Acris crepitans blan-Lescure, J. (1986b). Histoire de la classification des cecilies chardi): A test of the habitat acidification hypothesis. Copeia (Amphibia: Gymnophiona). Me´moires Socie ´teŹoologique 2006: 159–167.

de France 43: 11–19.

Lehtinen, R. M., Nussbaum, R. A., Richards, C. M., Cannatella, Lescure, J., Renous, S., and Gasc, J.-P. (1986). Proposition d’une D. C., and Vences, M.

(2007). Mitochondrial genes reveal nouvelle classification des amphibiens gymnopiones. Me´m-cryptic diversity in plant-breeding frogs from Madagascar oires Socie´teŹoologique de France 43: 145–177.

(Anura, Mantellidae, Guibemantis). Molecular Phylogenetics Lieb, C. S., Sites, J. W., and Archie, J. W. (1999). The use of iso-and Evolution 44: 1121–1129.

zyme characters in systematic studies of turtles: preliminary Lemaster, M. P., and Mason, R. T. (2002). Variation in a female data for Australian Chelids. Biochemical Systematics and sexual attractiveness pheromone controls male mate choice Ecology 27: 157–183.

in

garter

snakes.

Journal

of

Chemical

Ecology

28:

Liebman, P. A., and Granda, A. M. (1971). Microspectrophoto-1269–1285.

metric measurements of visual pigments in two species of LeMaster, M. P., Moore, I. T., and Mason, R. T. (2001). Conspe-turtle, Trachemys scripta and Chelonia mydas. Vision cific trailing behaviour of red-sided garter snakes, Thamno-Research 11: 105–114.

phis sirtalis parietalis, in the natural environment. Animal Liem, K. F., Marx, H., and Rabb, G. R. (1971). The viperid snake Behaviour 61: 827–833.

Azemiops: Its comparative cephalic anatomy and phyloge-Lemckert, F., and Brassil, T. (2003). Movements and habitat use netic position in relation to Viperinae and Crotalinae. Fieldi-by the giant burrowing frog, Heleioporus australiacus.

ana: Zoology 59: 1–126

ana: Zoology 55: 1–126.

Amphibia-Reptilia 24: 207–211.

Liem, S. S. (1970). The morphology, systematics, and evolution Lemmon, E. M., Lemmon, A. R., Collins, J. T., Lee-Yaw, J. A., of the Old World treefrogs (Rhacophoridae and Hyperolii-and Cannatella, D. C. (2007). Phylogeny-based delimitation dae). Fieldiana: Zoology 57: 1–145.

of species boundaries and contact zones in the trilling chorus Ligon, D. B., and Stone, P. A. (2003). Radiotelemetry reveals frogs (Pseudacris). Molecular Phylogenetics and Evolution terrestrial estivation in Sonoran Mud Turtles (Kinosternon 44: 1068–1082.

sonoriense). Journal of Herpetology 37: 750–754.

Lemos-Espinal, J. A., Smith, G. R., and Ballinger, R. E. (1998).

Lillywhite, H. B. (1970). Behavioral thermoregulation in the Thermal ecology of the crevice-dwelling lizard, Xenosaurus bullfrog. Copeia 1970: 158–168.

newmanorum. Journal of Herpetology 32: 141–144.

Lillywhite, H. B. (1987). Temperature, energetics, and physio-Lemos-Espinal, J. A., Smith, G. R., and Ballinger, R. E. (2003a).

logical ecology. In Snakes: Ecology and Evolutionary Biol-Ecology of Xenosaurus grandis agrenon, a knob-scaled liz-ogy. R. A. Seigel, J. T. Collins, and S. S. Novak (Eds.).

ard from Oaxaca, Me´xico. Journal of Herpetology 37: Pp. 422–477. Macmillian Publishing Co, New York.

192–196.

Lillywhite, H. B., and Maderson, P. F. A. (1982). Skin structure Lemos-Espinal, J., Smith, G. R., and Ballinger, R. E. (1997a).

and permeability. In Biology of the Reptilia. Volume 12.

Natural history of the Mexican knob-scaled lizard, Xeno-Physiology C.

C.

Gans

and

F.

H.

Pough

(Eds.).

saurus rectocollaris. Herpetological Natural History [1996]

Pp. 397–442. Academic Press, London.

4: 151–154.

Lima, A. P., and Caldwell, J. P. (2001). A new Amazonian spe-Lemos-Espinal, J., Smith, G. R., and Ballinger, R. E. (1997b).

cies of Colostethus with sky blue digits. Herpetologica 57: Neonate-female associations in Xenosaurus newmanorum: 180–189.

A case of parental care in a lizard? Herpetological Review Lima, A. P., Caldwell, J. P., and Biavati, G. M. (2002). Territo-28: 22–23.

rial and reproductive behavior of an Amazonian dendrobatid Lena, J. P., and de Fraipont, M. (1998). Kin recognition in the frog, Colostethus caeruleodactylus. Copeia 2002: 44–51.

common lizard. Behavioral Ecology and Sociobiology 42: Limpus, C. J. (1993). Family Dermochelyidae. In Fauna of Aus-341–347.

tralia. Volume 2A, Amphibia & Reptilia. C. J. Glasby, Lenk, P., Eidenmueller, B., Staudter, H., Wicker, R., and Wink, G. J. B. Ross, and P. I. Beesley (Eds.). Pp. 139–141. Austra-M. (2005). A parthenogenetic Varanus. Amphibia-Reptilia lian Government Public Service, Canberra.

26: 507–514.

Limpus, C. J., and Miller, J. D. (1993). Family Cheloniidae.

Leonard, W. P., Brown, H. A., Jones, L. L. C., McAllister, K. R., In Fauna of Australia. Volume 2A, Amphibia & Reptilia. C. J.

and Storm, R. M. (1993). Amphibians of Washington and Glasby, G. J. B. Ross, and P. I. Beesley (Eds.). Pp. 133–138.

Oregon. Seattle Audubon Soc, Seattle.

Australian Government Public Service, Canberra.

Australian Government Public Service, Canberra.

Lescure, J. (1968). Le comportement social des Batraciens.

Lindquist, E. D., and Hetherington, T. E. (1996). Field studies of Revue Comparatif Animal 2: 1–33.

visual and acoustic signaling in the “earless” Panamanian

golden frog, Atelopus zeteki. Journal of Herpetology 30: Lutz and J. A. Musick (Eds.). Pp. 107–135. CRC Press, Boca 347–354.

Raton, FL.

Lips, K. R. (1998). Decline of a tropical montane amphibian Lombard, R. E., and Sumida, S. S. (1992). Recent progress in fauna. Conservation Biology 12: 106–117.

understanding early tetrapods. American Zoologist 32: Lips, K. R. (1999). Mass mortality and population declines of 609–622.

anurans at an upland site in western Panama. Conservation Lombard, R. E., and Wake, D. B. (1976). Tongue evolution in Biology 13: 117–125.

the lungless salamanders, family Plethodontidae I. Introduc-Lips, K. R., Green, D. E., and Papendick, R. (2003). Chytridio-tion, theory, and a general model of dynamics. Journal of mycosis in wild frogs from southern Costa Rica. Journal of Morphology 148: 265–286.

Herpetology 37: 215–218.

Lombard, R. E., and Wake, D. B. (1977). Tongue evolution in Little, C. (1990). The Terrestrial Invasion. An Ecophysiological the lungless salamanders, family Plethodontidae II. Function Approach to the Origins of Land Animals. Cambridge Uni-and evolutionary diversity. Journal of Morphology 153: versity Press, Cambridge.

39–79.

Littlejohn, M. J., Roberts, J. D., Watson, G. F., and Davies, M.

Lombard, R. E., and Wake, D. B. (1986). Tongue evolution in (1993). The Myobatrachidae. In Fauna of Australia. Volume the lungless salamanders, family Plethodontidae. 4. Phylog 3A. Amphibia & Reptilia. C. J. Glasby, G. J. B.

family Plethodontidae. 4. Phylog-2A. Amphibia & Reptilia. C. J. Gasby, G. J. B. Ross, and eny of plethodontid salamanders and the evolution of feeding P. L. Beesley (Eds.). Pp. 41–57. Australian Government Pub-dynamics. Systematic Zoology 35: 532–551.

lishing Service, Canberra.

Lopez, C. H., and Brodie, E. D., Jr. (1977). The function of cos-Litzgus, J. D., Costanzo, J. P., Brooks, R. J., and Lee, R. E.

tal grooves in salamanders (Amphibia, Urodela). Journal of (1999). Phenology and ecology of hibernation in spotted Herpetology 11: 372–374.

turtles (Clemmys guttata) near the northern limit of their Lo´pez, P., Salvador, A., and Cooper, W. E., Jr. (1997). Discrim-range. Canadian Journal of Zoology 77: 1348–1357.

ination of self from other males by chemosensory cues in the Liu, C.-Z., and Hu, S.-Q. (1961). The Anura of China. Science amphisbaenian (Blanus cinereus). Journal of Comparative Press, Bejing. [in Chinese].

Psychology 111: 105–109.

Liu, F.-G. R., Moler, P. E., Whidden, H. P., Miyamoto, M. M., Losos, J. B. (1992). The evolution of convergent structure in

2004. Allozyme variation in the salamander genus Pseudo-

Caribbean Anolis communities. Systematic Biology 41: branchus: Phylogeographic and taxonomic signifcance.

403–420.

Copeia 2004: 136–144.

Losos, J. B. (1994). Integrative approaches to evolutionary ecol-Liu, F-G. R., Moler, P. E., and Miyamoto, M. M. (2006). Phylo-ogy: Anolis lizards as model systems. Annual Review of geography of the salamander genus Pseudobranchus in the Ecology and Systematics 25: 467–493.

southeastern United States. Molecular Phylogenetics and Losos, J. B., Jackman, T. R., Larson, A., de Queiroz, K., and Evolution 39: 149–159.

Rodrı´guez-Schettino, L. (1998). Contingency and determin-Llinaś, R., and Precht, W. (Eds.) (1976). Frog Neurobiology. A ism in replicated adaptive radiations of island lizards. Sci-Handbook. Springer-Verlag, Berlin.

ence 279: 2115–2118.

Lloyd, M., Inger, R. F., and King, F. W. (1968). On the diversity Lo¨tters, S. (1996). The Neotropical Toad Genus Atelopus. Check-of reptile and amphibian species in a Bornean rain forest, list-Biology-Distribution. M. Vences and F. Glaw Verlags American Naturalist 102: 497–515.

GbR, Ko¨ln.

Loader, S. P., Pisani, D., Cotton, J. A., Gower, D. J., Day, J. J., Lo¨tters, S., Jungfer, K.-H., and Widmer, A. 2000. A new genus and Wilkinson, M. (2007). Relative time scales reveal multi-of aposematic poison frog (Amphibia: Anura: Dendrobati-ple origins of parallel disjunct distributions of African caeci-dae) from the upper Amazon basin, with notes on its repro-lian amphibians. Biology Letters 3: 505–508.

ductive behaviour and tadpole morphology. Jahreshefte Loader, S. P., Wilkinson, M., Gower, D. J., and Msuya, C. A. (2003).

der Gesellschaft fu¨r Naturkunde in Wu¨rttemberg 156: A remarkable young Scolecomorphus vittatus (Amphibia: Gym-233–243.

nophiona: Scolecomorphidae) from the North Pare Mountains, Louw, G. N., and Holm, E. (1972). Physiological, morphological Tanzania. Journal of Zoology, London 259: 93–101.

and behavioural adaptations of the ultrapsammophilous, Lohmann, K. J. (1992). How sea turtles navigate. Scientific Namib Desert lizard Aporosaura anchietae (Bocage). Mado-American 266: 100–106.

qua, series II 1: 67–81.

Lohmann, K. J., Cain, S. D., Dodge, S. A., and Lohmann, Lovern, M. B., and Passek, K. M. (2002). Sequential alternation C. M. F. (2001). Regional magnetic fields as navigational of offspring sex from successive eggs by female green markers for sea turtles. Science 294: 364–366.

anoles, Anolis carolinensis. Canadian Journal of Zoology Lohmann, K. J., Lohmann, C. M. F., and Putman, N. F. (2007).

80: 77–82.

30: 77–82.

Magnetic maps in animals: Nature's GPS. Journal of Experi-Lovern, M. B., and Wade, J. (2003). Yolk testosterone varies mental Biology 210: 3697–3705.

with sex in eggs of the lizard. Anolis carolinensis. Journal Lohmann, K. J., Lohmann, C. M. F., Ehrhart, L. M., Bagley, of Experimental Zoology 295A: 206–210.

D. A., and Swing, T. (2004). Geomagnetic map used in Lowe, C. H., Schwalbe, C. R., and Johnson, T. B. (1986). The sea-turtle navigation. Nature 428: 909–910.

Venomous Reptiles of Arizona. Arizona Fish and Game Lohmann, K. J., Witherington, B. E., Lohmann, C. M. F., and Department, Phoenix.

Salmon, M. (1966). Orientation, navigation, and natal beach Lue, K. Y. (1991). The Amphibians of Taiwan. Taiwan Prov.

homing in sea turtles. In The Biology of Sea Turtles. P. L.

Dept. Education, Tapei.

Luiselli, L., Capula, M., and Shine, R. (1996). Reproductive out-Macey, J. R., Papenfuss, T. J., Kuehl, J. V., Fourcade, H. M., and put, costs of reproduction, and ecology of the smooth snake, Boore, J. L. (2004). Phylogenetic relationships among Coronella austriaca, in the eastern Italian Alps. Oecologia amphisbaenian reptiles based on complete mitochondrial 106: 100–110.

genomic sequences. Molecular Phylogenetics and Evolution Luiselli, L., Capula, M., and Shine, R. (1997). Food habits, 33: 22–31.

growth rates, and reproductive biology of grass snakes, Maderson, P. F. A. (1965). The structure and development of the Natrix natrix (Colubridae) in the Italian Alps. Journal of squamate epidermis. In Biology of the Skin and Hair Growth.

Zoology, London 241: 371–380.

A. G. Lyne and B. F. Short (Eds.). Pp. 129–153. Angus & Luppa, H. (1977).

Histology of the digestive tract. In Biology of Robertson, Sydney.

the Reptilia. Volume 6. Morphology E. C. Gans and T. S.

Maderson, P. F. A., Rabinowitz, T., Tandler, B., and Alibardi, L.

Parsons (Eds.). Pp. 225–313. Academic Press, London.

(1998). Ultrastructural contributions to an understanding of the Luthardt, G., and Roth, G. (1979). The relationship between cellular mechanisms involved in lizard skin shedding with com-stimulus orientation and stimulus movement pattern in the ments on the function and evolution of a unique lepidosaurian prey catching behavior of Salamandra salamandra. Copeia phenomenon. Journal of Morphology 236: 1–24.

1979: 442–447.

Madison, D. M. (1969). Homing behavior of the red-cheeked sal-Lutz, P. L. and Musick, J. A. (Eds.) (1996). The Biology of Sea amander, Plethodon jordani. Animal Behaviour 17: 25–39.

Turtles. CRC Press, Boca Raton, FL.

Madison, D. M., and Shoop, C. R. (1970). Homing behavior, ori-Lynch, J. D. (1971). Evolutionary relationships, osteology, and entation, and home range of salamanders tagged with Tanta-zoogeography of leptodactyloid frogs. Miscellaneous Publi-lum-182. Science 168: 1484–1487.

cations of the Museum of Natural History, University of Kan-Madsen, T. (1984). Movements, home range size and habitat use sas 53: 1–238.

of radio-tracked grass snakes (Natrix natrix) in southern Lynch, J. D. (1973). The transition from archaic to advanced Sweden. Copeia 1984: 707–713.

frogs. In Evolutionary Biology of the Anurans. J. L. Vial Madsen, T., and Shine, R. (1993). Male mating success and body (Ed.). Pp. 133–182. University of Missouri Press, Columbia.

size in European grass snakes. Copeia 1993: 561–564.

Lynch, J. D. (1978). A new eleutherodactyline frog from the Madsen, T., and Shine, R. (1994). Components of lifetime repro-Andes of northern Colombia (leptodactylidae). Copeia ductive success in adders, Vipera berus. Journal of Animal 1978: 17–21.

Ecology 63: 561–568.

Ecology 65: 501–508.

Lynch, J. D., Ruiz, P. M., and Rueda, J. V. (1983). Notes on the Madsen, T., and Shine, R. (1996). Seasonal migration of preda-distribution and reproductive biology of Centrolene geckoi-tors and prey—a study of pythons and rats in tropical Austra-deum Jimenez de la Espada in Colombia and Ecuador lia. Ecology 77: 149–156.

(Amphibia: Centrolenidae). Studies on Neotropical Fauna Madsen, T., Shine, R., Loman, J., and Hakansson, T. (1992).

and Environment 18: 239–243.

Why do female adders copulate so frequently? Nature 355: Lynn, W. G. (1970). The thryoid. In Biology of the Reptilia. Vol-440–441.

ume 3. Morphology C. C. Gans, and T. S. Parsons (Eds.).

Madsen, T., Ujvari, B., and Olsson, M. (2005). Old pythons stay Pp. 201–234. Academic Press, London.

fit: Effects of haematozoan infections on life history traits of MacArthur, R. H. (1984). Geographical Ecology: Patterns in the a large tropical predator. Oecologia 142: 407–412.

Distribution of Species. Princeton University Press, Prince-Maeda, N., and Matsui, M. (1989). Frogs and Toads of Japan.

ton, NJ.

Bun-Ichi Sogo Shuppan Co., Tokyo.

MacArthur, R. H., and Pianka, E. R. (1966). On optimal use of a Ma¨gdefrau, H. (1997). Biologie, Haltung und Zucht der Kroko-patchy environment. American Naturalist 100: 603–609.

dilschwanz-Ho¨ckerechse (Shinisaurus crocodilurus). Zeits-MacArthur, R. H., and Wilson, E. O. (1967). The Theory of chrift des Ko¨lner Zoo 2: 55–60.

Island Biogeography. Princeton University Press, Princeton, Maglia, A. M. (1996). Ontogeny and feeding ecology of the red-N.J.

backed salamander, Plethodon cinereus. Copeia 1996: Macdonald, L. A., and Mushinsky, H. R. 1988. Foraging ecology 576–586.

of the gopher tortoise, Gopherus polyphemus, in a sandhill Maglia, A. M. (1998). Phylogenetic relationships of extant pelo-habitat. Herpetologica 44: 345–

353.

batoid frogs (Anura: Pelobatoidea): Evidence from adult Macey, J. R. (2005). Plethodontid salamander mitochondrial morphology. Scientific Papers of the Natural History genomics: A parsimony evaluation of character conflict and Museum, University of Kansas 10: 1–19.

implications for historical biogeography. Cladistics 21: Maglia, A. M., Pugener, L. A., and Trueb, L. (2001). Compara-194–202.

tive development of anurans: Using phylogeny to understand Macey, J. R. J. A., Schulte, Larson, A., Tuniyev, B. S., Orlov, N., ontogeny. American Zoologist 41: 538–551.

and Papenfuss, T. J. (1999). Molecular phylogenetics, tRNA Magnusson, W. E. (1980). Hatching and creche formation by evolution, and historical biogeography in anguid lizards and Crocodylus porosus. Copeia 1980: 359–362.

related taxonomic families. Molecular Phylogenetics and Magnusson, W. E., Vliet, K. A., Pooley, A. C., and Whitaker, R.

Evolution 12: 250–272.

(1989). Reproduction. In Crocodiles and Alligators. C. A.

Macey, J. R., Larson, A., Ananjeva, N. B., and Papenfuss, T. J.

Ross (Ed.). Pp. 118–135. Golden Press Pty Ltd, Silverwater, (1997). Evolutionary shifts in three major structural features N.S.W.

of the mitochondrial genome among iguanian lizards. Jour-Mahmoud, I. Y., and Klicka, J. (1979). Feeding, drinking, and nal of Molecular Evolution 44: 660–674.

excretion. In Turtles, Perspectives and Research. M. Harless

and H. Morlock (Eds.). Pp. 229–243. John Wiley and Sons, Martin, K. L. M., and Sumida, S. S. (1997). An integrated New York.

approach to the origin of amniotes: Completing the transition Main, A. R., and Bull, C. M. (1996). Mother-offspring recogni-to land. In Amniote Origins: Completing the Transition to tion in two Australian lizards, Tiliqua rugosa and

Egernia Land. S. S. Sumida and K. L. M. Martin (Eds.). Pp. 1–8. Aca-stokesii. Animal Behaviour 52: 193–200.

demic Press, San Diego, CA.

Maiorana, V. C. (1977). Tail autotomy, functional conflicts and Martin, L. D. (1991). Mesozoic birds and the origin of birds.

their resolution by a salamander. Nature 265: 533–535.

In Origins of the Higher Groups of Tetrapods. Controversy Malkmus, R. (1995). Die Amphibien und Reptilien Portugals, and Consensus. H. P. Schultze and L. Trueb (Eds.).

Madeiras

und

der

Azoren.

Westarp

Wissenschaften,

Pp. 485–540. Comstock Publishing Associates, Ithaca, NY.

Magdeburg.

Martin, L. D., and Rothschild, B. M. (1989). Paleopathology and Manley, G. A. (1990). Peripheral Hearing Mechanisms in Rep-diving mosasaurs. American Scientist 77: 460–467.

tiles and Birds. Springer-Verlag, Berlin.

Martin, W. F., and Gans, C. (1972). Muscular control of the Manthey, U., and Grossmann, W. (1997). Amphibien & Reptilien vocal tract during release signaling in the toad Bufo valliceps.

Su¨dostasiens. Natur und Tier Verlag, Mu¨nster, Germany.

Journal of Morphology 137: 1–28.

Manzani, P. R., and Abe, A. S. (2002). A new species of Tupi-Martins, E. P. (1993). Contextual use of the push-up display by nambis Daudin, 1803 from southeastern Brazil. Arquivos do the sagebrush lizard, Sceloporus graciosus. Animal Beha-Museu Nacional, Rio de Janeiro 60: 295–302.

viour 45: 25–36.

Markwick, P. J. (1998). Fossil crocodilians as indicators of Late Martins, E. P. (1994). Phylogenetic perspectives on the evolution Cretaceous and Cenozoic climates: Implications for using of lizard territoriality. In Lizard Ecology: Historical and palaeontological

data

in

reconstructing

palaeoclimate.

Experimental Perspectives. L. J. Vitt and E. R. Pianka Palaeogeography, Palaeoclimatology, Palaeoecology 137: (Eds.). Pp. 118–144. Princeton University Press, Princeton, 205–271.

NJ.

Marmayou, J., Dubois, A., Ohler, A., Pasquet, E., and Tillier, A.

Martins, E. P., Labra, A., Halloy, M., and Thompson, J. T.

(2000). Phylogenetic relationships in the Ranidae. Indepen-

(2004). Large-scale patterns of signal evolution: An interspe-dent origin of direct development in the genera Philautus cific study of Liolaemus lizard headbob displays. Animal and Taylorana. Comptes Rendus De L Academie Des Behaviour 68: 453–463.

Sciences Serie Iii-Sciences De La Vie-Life Sciences 323: Martins, M. (2006). Life in the water: Ecology of the jacarerana 287–297.

lizard, Crocodilurus amazonicus. Herpetological Journal 16: Ma´rquez, R. (1992). Terrestrial paternal care and short breed-171–177.

ing seasons: reproductive phenology of the midwife toads Martins, M., and Oliveira, M. E. (1998). Natural history of Alytes obstetricans and A. cisternasii. Ecography 15: snakes in forests of the Manaus region, central Amazonia, 279–288.

Brazil. Herpetological Natural History 6: 78–150.

Ma´rquez, R. (1995). Female choice in the midwife toads (Alytes Martof, B. S. (1953). Home range and movements of the green obstetricans and A.

cisternasii). Behaviour 132: 151–161.

frog, Rana clamitans. Ecology 34: 529–543.

Ma´rquez, M. R. (1990). Sea turtles of the world. An annotated Martof, B. S. (1972). Pseudobranchus Gray. Catalogue of Amer-and illustrated catalogue of sea turtles species known to date.

ican Amphibians and Reptiles 118: 1–4.

Foof and Agriculture Organization of the United Nations Martof, B. S. (1974). Siren Linneaus. Catalogue of American Fisheries Synopsis 125/11: 1–81.

Amphibians and Reptiles 152: 1–2.

Marquez, R., and Bosch, J. (1997). Female preference in com-Marvin, G. A. (1996). Life history and population characteristics plex acoustical environments in the midwife toads Alytes of the salamander Plethodon kentucki with a review of obstetricans and Alytes cisternasii. Behavioral Ecology 8: Plethodon life histories. American Midland Naturalist 136: 588–594.

385–400.

Marquis, R. J., Donnelly, M. A., and Guyer, C. (1986). Aggrega-Maslin, T. P. (1950). The production of sound in caudate tions of calling males of Agalychnis calcifer Boulenger Amphibia. University of Colorado Studies, Series in Biology (Anura: Hylidae) in a Costa Rican lowland wet forest. Bio-No 1: 29–45.

tropica 18: 173–175.

Mason, R. T. (1992). Reptilian pheromones. In Biology of the Martin, J. (1992). Masters of Disguise: A Natural History of Reptilia. Volume 18, Physiology. Hormones, Brain, and Chameleons. Facts on File, Inc, New York.

Behavior. C. Gans and D. Crews (Eds.). Pp. 114–228. Uni-Martin, J. A., and Salvador, A. (1993). Tail loss reduces mating versity of Chicago Press, Chicago.

success in the Iberian rock-lizard, Lacerta monticola. Behav-Mason, R. T., and Crews, D. (1985). Female mimicry in garter ioral Ecology and Sociobiology 32: 185–189.

snakes. Nature 316: 59–60.

Martı́n, J., and Lopez, P. (1999). When to come out from a ref-Mason, R. T.

Martin, J., and Lopez, P. (1999). When to come out from a ref-Mason, R. T., and Crews, D. (1986). Pheromone mimicry in gar-uge: Risk-sensitive and state-dependent in an alpine lizard.

ter snakes. In Chemical Signals in Vertebrates. Volume 4.

Behavioral Ecology 10: 487–492.

Ecology, Evolution, and Comparative Biology. D. Duvall, Martin, K. L. M., and Nagy, K. A. (1997). Water balance and the D.

Müller-Schwarze,

and

R.

M.

Silverstein

(Eds.).

physiology

of

the

amphibian

to

amniote

transition.

Pp. 279–283. Plenum Press, New York.

In Amniote Origins. Completing the Transition to Land.

Masood-Parveez, U., and Nadkarni, V. B. (1993). The ovarian S. S. Sumida and K. L. M. Martin (Eds.). Pp. 399–423. Aca-cycle in an oviparous gymnophione amphibian Ichthyophis demic Press, San Diego.

beddomei (Peters). Journal of Herpetology 27: 59–63.

627

Massey, A. (1988). Sexual interactions in red-spotted newt popu-and morphological data. Molecular Phylogenetics and Evolu-lations. Animal Behaviour 36: 205–210.

tion 39: 16–32.

Masta, S. E., Sullivan, B. K., Lamb, T., and Routman, E. J.

McBrayer, L. D., and Reilly, S. M. (2002). Testing amniote mod-

(2002). Molecular systematics, hybridization, and phylogeo-els of prey transport kinematics: A quantitative analysis of graphy of the Bufo americanus complex in Eastern North mouth opening patterns in lizards. Zoology 105: 71–81.

America.

Molecular Phylogenetics

and

Evolution 24:

McBrayer, L. D., Corbin, C. E., Reilly, S. M., and Miles, D. B.

302–314.

(2007). Patterns of head shape variation in lizards: Morpho-Mathis, A. (1991). Territories of male and female terrestrial sal-logical correlates of foraging mode. In Lizard Ecology: The amanders: Costs, benefits, and intersexual spatial associa-Evolutionary Consequences of Foraging Mode. S. M. Reilly, tions. Oecologia 86: 433–440.

L. D. McBrayer, and D. B. Miles (Eds.). Pp. 271–301. Cam-Mathis, A., Jaeger, R. G., Keen, W. H., Ducey, P. K., Walls, bridge University Press, Cambrdge UK.

S. C., and Buchanan, B. W. (1995). Aggression and territori-McCarthy, C. J. (1985). Monophyly of elapid snakes (Serpentes: ality by salamanders and a comparison with the territorial Elapidae), an assessment of the evidence. Zoological Journal behaviour of frogs. In Amphibian Biology. Volume 2, Social of the Linnean Society 83: 79–93.

Behaviour. H. Heatwole and B. K. Sullivan (Eds.).

McCay, M. G. (2001). Aerodynamic stability and maneuverabil-Pp. 633–676. Surrey Beatty & Sons Pty Ltd., Chipping Nor-ity of the gliding frog Polypedates dennysi. Journal of Exper-ton Pty Ltd, N.S.W.

imental Biology 204: 2817–2826.

Matsui, M., ChanArd, T., and Nabhitabhata, J. (1996). Distinct McCay, M. G. (2003). Winds under the rain forest canopy: The specific status of Kalophrynus pleurostigma interlineatus aerodynamic environment of gliding tree frogs. Biotropica (Anura, Microhylidae). Copeia 1996: 440–445.

35: 94–102.

Mattison, C. (2007). The New Encyclopedia of Snakes. Cassell McClanahan, L. L. Jr., and Baldwin, R. (1969). Rate of water Illustrated, London.

uptake through the integument of the desert toad, Bufo punc-Mautz, W. J. (1982). Patterns of evaporative water loss.

tatus.

Comparative

Biochemistry

and

Physiology

28:

In Biology of Reptilia Volume 12, Physiology C: Physiologi-381–389.

cal Ecology. C. Gans and F. H. Pough (Eds.). Pp. 443–481.

McClanahan, L. L. Jr., Ruibal, R., and Shoemaker, V. H. (1983).

Academic Press, New York, NY.

Rate of cocoon formation and its physiological correlates in a Mautz, W. J., and Lopezforment, W. (1978). Observations on ceratophryd frog. Physiological Zoology 56: 430–435.

activity and diet of cavernicolous lizard Lepidophyma smithii McClanahan, L. L. Jr., Shoemaker, V. H., and Ruibal, R. (1976).

(Sauria: Xantusiidae). Herpetologica 34: 311–313.

Structure and function of the cocoon of a ceratophryd frog.

Mautz, W. J., and Nagy, K. A. (1987). Ontogenetic changes in Copeia 1976: 179–185.

diet, field metabolic-rate, and water flux in the herbivorous McClanahan, L. L. Jr., Stinner, J. N., and Shoemaker, V. H.

lizard Dipsosaurus dorsalis. Physiological Zoology 60: (1978). Skin lipids, water loss, and metabolism in a South 640–657.

American tree frog (Phyllomedusa sauvagei). Physiological Maxson, L. R., and Maxson, R. D. (1990). Proteins II: immuno-Zoology 51: 179–187.

logical techniques. In Molecular Systematics, Second Edi-Mccord, W. P., and Thomson, S. A. (2002). A new species of tion. D. M. Hillis, C. Moritz, and B. K. Mable (Eds.).

Chelodina (Testudines: Pleurodira: Chelidae) from northern Pp. 127–155. Sinauer Associates, Inc, Sunderland, MA.

Australia. Journal of Herpetology 36: 255–267.

Maxson, L. R., and Ruibal, R. (1988). Relationships of frogs in McCord, W. P., Ouni, M. J., and Lamar, W. W. (2001). A taxo-the leptodactylid subfamily Ceratophryinae. Journal of Her-nomic reevaluation of Phrynops (Testudines: Chelidae) with petology 22: 228–231.

the description of two new genera and a new species of Maxson, R. D., and Maxson, L. R. (1986). Micro-complement Batrachemys. Revista de Biologıá Tropical, San Jose´ 49: fixation: A quantitative estimator of protein evolution.

715–764.

Molecular Biology and Evolution 3: 375–388.

McCoy, C. J. (1968). Reproductive cycles and viviparity in Gua-Mayer, W., and Benyr, G. (1994). Albumin-Evolution und Phy-temalan Corythophanes percarinatus (Reptilia: Iguanidae).

logenese in der Familie Lacertidae (Reptilia: Sauria).

Herpetologica 24: 175–178.

Annalen des Naturhistorischen Museums in Wien 96B: McCue, M. D. (2004). General effects of temperature on animal 621–648.

(2004). General effects of temperature on animal 621–648.

biology. In Temperature-Dependent Sex Determination in Mayer, W., and Bishoff, W. (1996). Beitra¨ge zur taxonomischen Vertebrates. N. Valenzuela and V. Lance (Eds.). Pp. 71–78.

Revision der Gattung Lacerta (Reptilia: Lacertidae). Teil 1: Smithsonian Books, Washington, D. C.

Zootoca, Omanosaura, Timon and Teira als eigensta¨ndige McDiarmid, R. W. (1978). Evolution of parental care in frogs.

Gattungen. Salamandra 32: 163–170.

In The Development of Behavior: Comparative and Evolu-Mayr, E., and Ashlock, S. D. (1991). Principles of Systematic tionary Aspects. G. M. Burghardt and M. Bekoff (Eds.).

Zoology. McGraw-Hill Book Co, New York.

Pp. 127–147. Garland STPM Press, New York.

Mazzotti, F. J., and Dunson, W. A. (1989). Osmoregulation in McDiarmid, R. W., Campbell, J. A., and Toure´, T. A. (1999).Snake crocodilians. American Zoologist 29: 903–920.

Species of the world. A Taxonomic and Geographic Reference McAliley, L. R., Willis, R. E., Ray, D. A., White, P. S., Brochu, Volume 1. The Herpetologists’ League, Washington, D.C.

C. A., and Densmore, L. D. (2006). Are crocodiles really McDonald, K. R., and Tyler, M. J. (1984). Evidence of gastric monophyletic? Evidence for subdivisions from sequence brooding in the Australian leptodactylid frog Rheobatrachus

vitellinus. Transactions of the Royal Society of South Austra-Measey, G. J., and Tinsley, R. C. (1997). Mating behavior of lia 108: 226.

Xenopus wittei (Anura: Pipidae). Copeia 1997: 601–609.

McDowell, S. B. (1969). Notes on the Australian seas-snake Medica, P. A., and Turner, F. B. (1984). Natural longevity of Ephalophis greyi M. Smith (Serpentes: Elapidae, Hydrophii-lizards in southern Nevada. Herpetological Review 15: nae) and the origin and classification of sea-snakes. Zoologi-34–35.

cal Journal of the Linnean Society 48: 333–349.

Medica, P. A., Bury, R. B., and Luckenbach, R. A. (1980).

McDowell, S. B. (1974). A catalogue of the snakes of New Drinking and construction of water catchments by the desert Guinea and the Solomons, with special reference to those tortoise, Gopherus agassizii, in the Mojave Desert. Herpeto-in the Bernice P. Bishop Museum, part I. Scolecophidia.

logica 36: 301–304.

Journal of Herpetology 8: 1–128.

Meffe, G. K. (1994). Human population control: The missing McDowell, S. B. (1987). Systematics. In Snakes: Ecology and awareness. Conservation Biology 8: 310–313.

Evolutionary Biology. R. A. Seigel, J. T. Collins, and S. S.

Meffe, G. K. and Carroll, C. R. (Eds.) (1994). Principles of Con-Novak (Eds.). Pp. 3–50. MacMillan, New York.

servation Biology. Sinauer Associates, Inc., Sunderland, MA.

McDowell, S. B., Jr. (1964). Partition of the genus Clemmys and Meffe, G. K., Carroll, C. R., and Pimm, S. L. (1994). Commu-related problems in the taxonomy of the aquatic Testudini-nity-level conservation: species interactions, disturbance dae. Proceedings of the Zoological Society of London 143: regimes, and invading species. In Principles of Conservation 239–279.

Biology. G. K. Meffe and C. R. Carroll (Eds.). Pp. 209–236.

McGowan, C. (1991). Dinosaurs, Spitfires, and Sea Dragons.

Sinauer Associates, Inc, Sunderland, MA.

Harvard University. Press, Cambridge, Mass.

Meffe, G. K., Ehrenfeld, D., and Noss, R. F. (2006). Conserva-McGowan, G., and Evans, S. E. (1995). Albanerpetontid amphi-tion biology at twenty. Conservation Biology 20: 595–596.

bians from the Cretaceous of Spain. Nature 373: 143–145.

Meffe, G. K., Ehrlich, A. H., and Ehrenfeld, D. (1993). Human-McGregor, J. H., and Teska, W. R. (1989). Olfaction as an orien-population control: The missing agenda. Conservation Biol-tation mechanism in migrating Ambystoma maculatum.

ogy 7: 1–3.

Copeia 1989: 779–781.

Melisch, R. (1998). Wildlife trade, sustainable use, and conserva-McGuire, J. A. (1996). Phylogenetic systematics of crotaphytid tion implications from a WWF and TRAFFIC perspective.

lizards (Reptilia: Iguania: Crotaphytidae). Bulletin of the In Conservation, Trade and Sustainable Use of Lizards and Carnegie Museum of Natural History 32: 1–143.

Snakes in Indonesia. W. Erdelen (Ed.). Pp. 1–8. Mertensiella McGuire, J. A. (2003). Allometric prediction of locomotor per-7, Rheinbach, Germany.

formance: An example from Southeast Asian flying lizards.

Mendelson, J. R., III, Lips, K. R., Gagliardo, R. W., Rabb, G. B., American Naturalist 161: 337–349.

Collins, J. P., Diffendorfer, J. E., Daszak, P., Ibanez, R., Zip-McGuire, J. A., and Dudley, R. (2005). The cost of living large: pel, K. C., Lawson, D. P., Wright, K. M., Stuart, S. N., Gas-Comparative gliding performance in flying lizards (Agami-con, C., da Silva, H. R., Burrowes, P. A., Joglar, R. L., La dae: Draco). American Naturalist 166: 93–106.

Marca, E., Lotters, S., du Preez, L. H., Weldon, C., Hyatt, McGuire, J. A., and Heang, K. B. (2001). Phylogenetic systemat-A., Rodriguez-Mahecha, J. V., Hunt, S., Robertson, H., Lock, ics of southeast Asian flying lizards (Iguania: Agamidae: B., Raxworthy, C. J., Frost, D. R., Lacy, R. C., Alford, R. A., Draco) as inferred from mitochondrial DNA sequences.

Campbell, J. A., Parra-Olea, G., Bolanos, F., Domingo, Biological Journal of the Linnean Society 72: 203–229.

the Linnean Society 72: 203–229.

J. J. C., Halliday, T., Murphy, J. B., Wake, M. H., Coloma, McGuire, J. A., Linkem, C. W., Koo, M. S., Hutchison, D. W., Lap-L. A., Kuzmin, S. L., Price, M. S., Howell, K. M., Lau, M., pin, A. K., Orange, D. I., Lemos-Espinal, J., Riddle, B. R., and Pethiyagoda, R., Boone, M., Lannoo, M. J., Blaustein, Jaeger, J. R. (2007). Mitochondrial introgression and incom-A. R., Dobson, A., Griffiths, R. A., Crump, M. L., Wake, plete lineage sorting through space and time: Phylogenetics of D. B., and Brodie, E. D. (2006). Biodiversity—Confronting crotaphytid lizards. Evolution 61: 2879–2897.

amphibian declines and extinctions. Science 313: 48.

McIlhenny, E. A. (1935). The Alligator's Life History. Christo-Menezes, V. A., Rocha, C. F. D., and Dutra, D. F. (2004). Repro-pher Publ. House, Boston.

ductive ecology of the parthenogenetic whiptail lizard Cne-McIntyre, N. E., and Wiens, J. A. (1999). Interactions between midophorus nativo in a Brazilian restinga habitat. Journal landscape structure and animal behavior: The roles of hetero-of Herpetology 38: 280–282.

geneously distributed resources and food deprivation on Menin, M., Rodrigues, D. d. J., and de Azevedo, C. S. (2005).

movement patterns. Landscape Ecology 14: 437–447.

Predation on amphibians by spiders, (Arachnida, Araneae) McPherson, R. J., and Marion, K. R. (1981). The reproductive in the Neotropical region. Phyllomedusa 4: 39–47.

biology of female Sternotherus odoratus in an Alabama pop-Menzies, J. I. (1976). Handbook of Common New Guinea Frogs.

ulation. Journal of Herpetology 15: 389–396.

Wau Ecological Institute Handbook No. 1, Wau.

McVey, M. E., Zahary, R. G., Perry, D., and MacDougal, J.

Mertens, R., and Wermuth, H. (1960). Die Amphibien und Rep-

(1981). Territoriality and homing behavior in the poison dart tilien Europas. Verlag Waldemar Kramer, Frankfurt am frog (Dendrobates pumilio). Copeia 1981: 1–8.

Main.

Means, D. B. (1996). Amphiuma pholeter Neill. Catalogue of Mesquita, D. O., Colli, G. R., Franc¸a, F. G. R., and Vitt, L. J.

American Amphibians and Reptiles 622: 1–2.

(2006). Ecology of a Cerrado lizard assemblage in the Jala-Means, D. B., Palis, J. G., and Baggett, M. (1996). Effects of pa˜o region of Brazil. Copeia 2006: 460–471.

slash pine silviculture on a Florida population of flatwoods Metter, D. E. (1967). Variation in the Ribbed Frog Ascaphus salamanders. Conservation Biology 10: 426–437.

truei Stejneger. Copeia 1967: 634–649.

Metter, D. E. (1968). Ascaphus and A. truei. Catalogue of Amer-Milton, T. H., and Jenssen, T. A. (1979). Description and signifi-ican Amphibians and Reptiles 69: 1–2.

cance of vocalizations by Anolis grahami. Copeia 1979: Meyers, J. J., O’Reilly, J. C., Monroy, J. A., and Nishikawa, 481–489.

K. C. (2004). Mechanism of tongue protraction in microhylid Min, M. S., Yang, S. Y., Bonett, R. M., Vieites, D. R., Brandon, frogs. Journal of Experimental Biology 207: 21–31.

R. A., and Wake, D. B. (2005). Discovery of the first Asian Meylan, P. A. (1987). The phylogenetic relationships of soft-plethodontid salamander. Nature 435: 87–90.

shelled turtles (Family Trionychidae). Bulletin of the Ameri-Minnich, J. E. (1979). Reptiles. In Comparative Physiology of can Museum of Natural History 186: 1–110.

Osmoregulation

in

Animals.

G.

M.

Hughes

(Ed.).

Meylan, P. A. (1996). Skeletal morphology and relationships of Pp. 391–641. Academic Press, London.

the Early Cretaceous side-necked turtle, Araripemys barretoi Minnich, J. E. (1982). The use of water. In Biology of the Repti-

(Testudines: Pelomedusoides: Araripemydidae), from the lia (Volume 12): Physiology C (Physiological Ecology). C.

Santana Formation of Brazil. Journal of Vertebrate Paleon-Gans and F. H. Pough (Eds.). Pp. 325–395. Academic Press, tology 16: 20–33.

London.

Meylan, P. A., and Gaffney, E. S. (1989). The skeletal morphol-Mitchell, J. C. (1988). Population ecology and life histories of the ogy of the Cretaceous cryptodiran turtle, Adocus, and the freshwater turtles, Chrysemys picta and Sternotherus odoratus relationships of the Trionychoidea. American Museum Novi-in an urban lake. Herpetological Monographs 2: 40–61.

tates 2941: 1–60.

Mitchell, J. C. (1994). The Reptiles of Virginia. Smithsonian Miaud, C., Andreone, F., Riberon, A., De Michelis, S., Clima, Institute Press, Washington, D.C.

V., Castanet, J., Francillon-Vieillot, H., and Guyetant, R.

Mitchell, J. C., and Beck, R. A. (1992). Free-ranging domestic (2001). Variations in age, size at maturity and gestation dura-cat predation on native vertebrates in rural and urban Virgi-tion among two neighbouring populations of the alpine sala-nia. Virginia Journal of Science 43: 197–207.

mander (Salamandra lanzai). Journal of Zoology, London Mitchell, S. L., and Altig, R. (1983). The feeding ecology of Soo-254: 251–260.

glossus gardineri. Journal of Herpetology 17: 281–282.

Middendorf, G. A., and Sherbrooke, W. C. (1992). Canid elicita-Mittermeier, R. A. (1972). Jamaica’s endangered species. Oryx tion of blood squirting in a horned lizard. Copeia 1992: 11: 258–262.

519–527.

Mittermeier, R. A., Myers, N., and Mittermeier, C. G. 2000.

Milius, S. (2006). No-dad dragons: Komodos reproduce without Hotspots: Earth's biologically richest and most endangered males. Science News 170: 403.

terrestrial

ecoregions.

CEMEX,

Conservation

Miller, J. D. (1996). Reproduction in sea turtles. In The Biology International.

of Sea Turtles. P. L. Lutz and J. A. Musick (Eds.).

Mlynarski, M. (1976). Testudines. Handbuch der Palaöherpeto-Pp. 51–81. CRC Press, Boca Raton, FL.

logie, 7. Gustav Fischer Verlag, Stuttgart.

Miller, J. R. (2005). Biodiversity conservation and the extinction Modha, M. L. (1967). The ecology of the Nile crocodile (Croco-of experience. Trends in Ecology & Evolution 20: 430–434.

dylus niloticus Laurenti) on Central Island, Lake Rudolf.

Miller, M. R. (1954). Further observations on reproduction in the East African Wildlife Journal 5: 74–95.

lizard Xantusia vigilis. Copeia 1954: 38–40.

Moler, P. E., and Kezer, J. (1993). Karyology and systematics of Miller, M. R., and Lagios, M. D. (1970). The pancreas.

the salamander genus Pseudobranchus (Sirenidae). Copeia In Biology of the Reptilia. Volume 3. Morphology C. C. Gans 1993: 39–47.

and T. S. Parsons (Eds.). Pp. 319–346. Academic Press, Moll, D. (1980). Natural history of the river terrapin, Batagar London.

baska (Gray) in Malaysia (Testudines: Emydidae). Malaya-Mills, M. S., Hudson, C. L., and Berna, H. J. (1995). Spatial sian Journal of Science 6: 23–62.

ecology and movements of the brown water snake (Nerodia Moll, D. (1989). Food and feeding behavior of the turtle, Dermat-taxispilota). Herpetologica 51: 412–423.

emys mawei, in Belize. Journal of Herpetology 23: 445–447.

Milner, A. C. (1988). The relationships and origin of living Moll, D. (1990). Population sizes and foraging ecology in a trop-amphibians. In The Phylogeny and Classification of the Tet-ical freshwater stream turtle community. Journal of Herpe-rapods. Vol. 1: Amphibians, Reptiles, Birds. M. J. Benton tology 24: 48–53.

(Ed.). Pp. 59–102. Clarendon Press, Oxford.

Moll, D., and Klemens, M. W. (1996). Ecological characteristics Milner, A. C. (1980). A review of them Nectridea (Amphibia).

of the pancake tortoise, Malacochersus tornieri, in Tanzania.

In The Terrestrial Environment and the Origin of Land Ver-Chelonian Conservation Biology 2: 26–35.

tebrates. A. L. Panchen (Ed.). Pp. 377–405. Academic Press, Moll, E. O., and Legler, J. M. (1971). The life history of a Neo-London.

tropical slider turtle, Pseudemys scripta (Schoepff) in Pan-Milner, A. C. (1994). Late Triassic and Jurassic amphibians: Fos-ama. Bulletin of the Los Angeles County Museum of sil record and phylogeny. In the shadow of the dinosaurs.

Science 11: 1–102.

Early Mesozoic Tetrapods. N. C. Fraser and H.-D. Sues Monagas, W. R., and Gatten, R. E., Jr. (1983). Behavioural fever (Eds.). Pp. 23–37. Cambridge University Press, New York.

in the turtles Terrapene carolina and Chrysemys picta. Jour-Milner, A. R. (1993). The Paleozoic relatives of lissamphibians.

nal of Thermal Biology 8: 285–288.

Herpetological Monographs 7: 8–27.

Montanucci, R. R. (1974). Convergence, polymorphism or intro-Milner, A. R., Smithson, T. R., Milner, A. C., Coates, M. I., and gressive hybridization:

R., Smithson, T. R., Milner, A. C., Coates, M. I., and gressive hybridization. Analysis of interaction between Cro-Rolfe, W. D. I. (1986). The search for early tetrapods. Mod-taphytus collaris and Crotaphytus reticulatus (Sauria: ern Geology 10: 1–28.

Iguanidae). Copeia 1974: 87–101.

Mook, C. C. (1921). Notes on the postcranial skeleton in Croco-

(Ed.). Pp. 19–23. Herpetological Association of Africa, dilia. Bulletin of the American Museum of Natural History Matieland, S. Afr.

44: 67–100.

Mrosovsky, N. (1983). Conserving Sea Turtles. British Herpeto-Moon, B. R. (2000). The mechanics and muscular control of con-logical Society, London.

striction in gopher snakes (Pituophis melanoleucus) and a Mrosovsky, N. (1994). Sex ratios in sea turtles. Journal of Exper-king snake (Lampropeltis getula). Journal of Zoology, Lon-imental Zoology 270: 16–27.

don 252: 83–98.

Mueller, H. (2006). Ontogeny of the skull, lower jaw, and hyo-Morafka, D. J. (1994). Neonates: Missing links in the life his-branchial skeleton of Hypogeophis rostratus (Amphibia: tories of North American tortoises. U S Fish and Wildlife Gymnophiona: Caeciliidae) revisited. Journal of Morphology Service Fish and Wildlife Research 13: 161–173.

267: 968–986.

Morales, V. R., and McDiarmid, R. W. (1996). Annotated check-Mueller, R. L., Macey, J. R., Jaekel, M., Wake, D. B., and Boore, list of the amphibians and reptiles of Pakita, Manu National J. L. (2004). Morphological homoplasy, life history evolu-Park Reserve Zone, with comments on the herpetofauna of tion, and historical biogeography of plethodontid salaman-Madre de Dios. In Manu. The Biodiversity of Southeastern ders

inferred

from

complete

mitochondrial

genomes.

Peru. D. E. Wilson and A. Sandoval (Eds.). Pp. 503–522.

Proceedings of the National Academy of Sciences (USA) Smithsonian Institute, Washington, D. C.

101: 13820–13825.

Morey, S. R. (1990). Microhabitat selection and predation in the Mu¨ller, R., Lutzmann, N., and Walbro¨l, U. (2004). Furcifer par-Pacific treefrog, Pseudacris regilla. Journal of Herpetology dalis—Das Pantherchama¨leon. Natur und Tier Verlag, 24: 292–296.

Mu¨nster, Germany.

Morgan, J. A. T., Vredenburg, V. T., Rachowicz, L. J., Knapp, Murphy, J. B., Quinn, H, and Campbell, J. A. (1977). Observa-R. A., Stice, M. J., Tunstall, T., Bingham, R. E., Parker, tions on the breeding habits of the aquatic caecilian Typhlo-J. M., Longcore, J. E., Moritz, C., Briggs, C. J., and Taylor, nectes compressicaudus. Copeia 1977: 66–69.

J. W. (2007). Population genetics of the frog-killing fungus Murphy, J. C., and Voris, H. K. (1994). A key to the homalop-Batrachochytrium dendrobatidis.

Proceedings

of

the

sine snakes. The Snake 26: 123–133.

National Academy of Sciences (USA) 104: 13845–13850.

Murphy, P. J. (2003a). Context-dependent reproductive site choice Mori, A. (1996). A comparative study of the development in a Neotropical frog. Behavioral Ecology 14: 626–633.

of prey handling behavior in young rat snakes, Elaphe Murphy, P. J. (2003b). Does reproductive site choice in a Neo-quadrivirgata and E. climacophora. Herpetologica 52: tropical frog mirror variable risks facing offspring? Ecologi-

313–322.

cal Monographs 73: 45–67.

Morin, P. J. (1987). Predation, breeding asunchrony, and the out-Murphy, R. W., Sites, J. W., Buth, D. G., and Haufler, C. H.

come of competition among treefrog tadpoles. Ecology 68: (1996). Proteins: Isozyme electrophoresis. In Molecular Sys-675–683.

tematics (Second Edition). D. M. Hillis, C. Moritz, and B. K.

Moritz, C., and Hillis, D. M. (1996). Molecular systematics: con-Mable (Eds.). Pp. 51–120. Sinauer Associates, Inc., Sunder-text and controversies. In Molecular Systematics. Second land, MA.

Edition. D. M. Hillis, C. Moritz, and B. K. Mable (Eds.).

Mushinsky, H. R., Hebrard, J. J., and Vodopich, D. S. (1982).

Pp. 1–13. Sinauer Associates, Inc, Sunderland, MA.

Ontogeny of water snake foraging ecology. Ecology 63: Moritz, C., Patten, J. L., Schneider, C. J., and Smith, T. B.

1624–1629.

(2000). Diversification of rainforest faunas: an integrated Myers, C. W., and Daly, J. W. (1983). Dart-poison frogs. Scien-molecular approach. Annual Reviews of Ecology and System-tific American 248: 120–133.

atics 31: 533–563.

Myers, C. W., and Rand, A. S. (1969). Checklist of amphibians Morreale, S. J., Ruiz, G. J., Spotila, J. R., and Standora, E. A.

and reptiles of Barro Colorado Island, Panama, with com-

(1982). Temperature-dependent sex determination: Current ments on faunal change and sampling. Smithsonian Contribu-practices threaten conservation of sea turtles. Science 216: tions to Zoology 10: 1–11.

1245–1247.

Myers, C. W., Paolillo, O. A., and Daly, J. W. (1991). Discovery Mosher, H. S., Fischer, H. G., Fuhrman, F. A., and Buchwald, of a defensively malodorous and nocturnal frog in the family H. D. (1964). Tarichatoxin-tetrodotoxin - potent neuro-Dendrobatidae: phylogenetic significance of a new genus and toxin:

neuro Dendrobatidae: phylogenetic significance of a new genus and toxin. Nonprotein substance isolated from California species from the Venezuelan Andes. American Museum newt is same as toxin from puffer fish. Science 144: Novitates 3022: 1–33.

1100–1110.

Myers, E. M., and Zamudio, K. R. (2004). Multiple paternity in Moskovits, D. K., and Bjorndal, K. (1990). Diet and Food Prefer-an aggregate breeding amphibian: the effect of reproductive ences of the tortoises Geochelone carbonaria and G. denticu-skew on estimates of male reproductive success. Molecular lata in northwestern Brazil. Herpetogica 46: 207–218.

Ecology 13: 1951–1963.

Motychak, J. E., and Brodie, E. D. (1999). Evolutionary response Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonesca, of predators to dangerous prey: Preadaptation and the evolu-G. A. B., and Kent, J. (2000). Biodiversity hotspots for con-tion of tetrodotoxin resistance in garter snakes. Evolution 53: servation priorities. Nature 403: 853–858.

1528–1535.

Nagy, K. A. (1972). Water and electrolyte budgets of a free-liv-Mouton, P. le F. N. (1997). Family Cordylidae. In Proceedings of ing desert lizard, Sauromalus obesus. Journal of Compara-the Fitzsimons Commemorative Symposium. J. H. van Dyke tive Physiology B 79: 39–62.

Nagy, K. A. (1982). Field studies of water relations. In Biology islands, aldermen group, New Zealand. New Zealand Journal of the Reptilia (Volume 12): Physiology C (Physiological of Zoology 17: 153–156.

Ecology). C. Gans and F. H. Pough (Eds.) Pp. 483–501. Aca-Newman, D. G., Watson, P. R., and McFadden, I. (1994). Egg-demic Press, London.

production by tuatara on Lady Alice and Stephens Island, Nagy, K. A. (1983a). The doubly labeled water (3H18O) method: New-Zealand. New Zealand Journal of Zoology 21: 387–398.

a guide to its use. University of California, Los Angeles. Pub-Newman, D.

a guide to its use. University of California, Los Angeles, Pub Newman, D. G., Watson, P. R., Grigg, G., Shine, R., and lication 12–1417: 1–45.

Ehmann, H. (1985). The contribution of radiography to the Nagy, K. A. (1983b). Ecological energetics. In Lizard Ecology: study of the reproductive ecology of the tuatara, Sphenodon Studies of a Model Organism. R. B. Huey, E. R. Pianka, punctatus. In Biology of Austrasian Frogs and Reptiles.

and T. W. Schoener (Eds.). Pp. 25–54. Harvard University G. Grigg, R. Shine, and H. Ehmann (Eds.). Pp. 7–10. Surrey Press, Cambridge, Mass.

Beatty & Sons Pty Ltd, Chipping Norton Pty Ltd., Sydney, Nagy, K. A., and Medica, P. A. (1986). Physiological ecology of Australia.

desert tortoises in southern Nevada. Herpetologica 42: Newton, W. D., and Trauth, S. E. (1992). Ultrastructure of the 73–92.

spermatozoon of the lizard Cnemidophorus sexlineatus Nagy, K. A., Huey, R. B., and Bennett, A. F. (1984). Field ener-

(Sauria: Teiidae). Herpetologica 48: 330–343.

getics and foraging mode of Kalahari lacertid lizards. Ecol-Nicholson, K. E. (2002). Phylogenetic analysis and a test of the ogy 65: 588–596.

current infrageneric classification of Norops (beta Anolis).

Nagy, Z. T., Vidal, N., Vences, M., Branch, W. R., Pauwels, Herpetological Monographs 16: 93–120.

O. S. G., Wink, M., and Joger, U. (2005). Molecular sys-Nickerson, M. A., and May, C. E. (1973). The hellbenders: North temaics of African Colubroidea (Squamata: Serpentes).

American giant salamanders. Milwaukee Public Museum, In African Biodiversity: Molecules, Organisms, Ecosystems, Publications in Biology and Geology 1: 1–106.

Proceedings of the 5th International Symposium on Tropical Nielsen, R. (2005). Molecular signatures of natural selection.

Biology. B. A. Huber, B. J. Sinclair, and e Lampe K. H.

Annual Review of Genetics 39: 197–218.

(eds.). Pp. 221–228. Museum Koenig, Bonn.

Nielsen, M., Lohman, K., and Sullivan, J. (2001). Phylogeography

Nielson, M., Lohman, K., and Sullivan, J. (2001). Phylogeography Nanayakkara, G. L. A. (1988). An analysis of the defensive of the tailed frog (Ascaphus truei): Implications for the bioge-behaviour of the Sri Lankan pipe snake, Cylindrophis macu-ography of the Pacific Northwest. Evolution 55: 147–160.

latus (Linne, 1758). The Snake 20: 81–83.

Niewiarowski, P. H. (1994). Understanding geographic life-his-National Research Council (1990). Decline of the Sea Turtles.

tory variation in lizards. In Lizard Ecology: Historical and National Academy Press, Washington, D.C.

Experimental Perspectives. L. J. Vitt and E. R. Pianka Narahashi, T. (2001). Pharmacology of tetrodotoxin. Journal of (Eds.). Pp. 31–49. Princeton University Press, Princeton NJ.

Toxicology-Toxin Review 20: 67–84.

Niewiarowski, P. H., Congdon, J. D., Dunham, A. E., Vitt, L. J., Navas, C. A., and Chaui-Berlinck, J. G. (2007). Respiratory and Tinkle, D. W. (1997). Tales of lizard tails: Effects of tail physiology of high-altitude anurans: 55 years of research on autotomy on subsequent survival and growth of free-ranging altitude and oxygen. Respiratory Physiology & Neurobiology hatchling Uta stansburiana. Canadian Journal of Zoology 158: 307–313.

75: 542–548.

Near, T. J., Meylan, P. A., and Shaffer, H. B. (2005). Assessing Noble, G. K. (1922). The phylogeny of the Salientia. I. The oste-concordance of fossil calibration points in molecular clock ology and the thigh musculature; their bearing on classifica-studies: An example using turtles. American Naturalist 165: tion and phylogeny. Bulletin of the American Museum of 137–146.

Natural History 46: 1–87.

Necas, P. (2004). Chameleons, Nature's Hidden Jewels. Edition Noble, G. K. (1925). The integumentary, pulmonary, and cardiac Chimaira, Frankfurt am Main.

modifications correlated with increased cutaneous respiration Necas, P., and Schmidt, W. (2004). Stump-tailed Chameleons.

in the Amphibia: A solution of the 'hairy frog' problem.

Miniature Dragons of the Rainforest. Edition Chimaira, Journal of Morphology and Physiology, 40: 341–416.

Frankfurt, Germany.

Noble, G. K. (1931). The Biology of the Amphibia. McGraw-Hill Nei, M., and Kumar, S. (2000). Molecular Evolution and Phylo-Book Co, New York, NY.

genetics. Oxford University Press, New York.

Noble, G. K., and Bradley, H. T. (1933). The mating behavior of Nelsen, O. E. (1953). Comparative Embryology of the Verte-lizards; Its bearing on the theory of sexual selection. Annals brates. Blakiston Co., Inc, New York.

of the New York Academy of Sciences 35: 25–100.

Nelson, N. J., Thompson, M. B., Pledger, S., Keall, S. N., and Noble, G. K., and Clausen, H. J. (1936). The aggregation behav-Daugherty, C. H. (2004). Egg mass determines hatchling ior of Storeria dekayi and other snakes, with especial refer-size, and incubation temperature influences post-hatching ence to the sense organs involved. Ecological Monographs growth, of tuatara Sphenodon punctatus. Journal of Zoology, 6: 271–316.

London 263: 77–87.

Noble, G. K., and Mason, E. R. (1933). Experiments on the Newman, D. G. (1987). Burrow use and population densities of brooding habits of the lizards Eumeces and Ophisaurus.

tuatara (Sphenodon punctatus) and how they are influenced American Museum Novitates 619: 1–29.

by fairy prions (Pachyptila turtur) on Stephens Island, New Nogueira, C, Paula H. Valdujo, P. H., and Franc¸a, F. G. R. Habi-Zealand. Herpetologica 43: 336–344.

tat variation and lizard diversity in a Cerrado area of Central Newman, D. G., and McFadden, I. (1990). Status of the tuatara, Brazil. Studies on Neotropical Fauna and Environment 40: Sphenodon punctatus, on Hongiora and Ruamahua-Iti 105–112.

Nokhbatolfoghahai, A., and Downie, J. R. (2007). Amphibian Nussbaum, R. A. (1985b). Amphibian fauna of the Seychelles hatching gland cells: Pattern and distribution in anurans. Tis-Archipelago. National Geographic Society Research Reports sue & Cell 39: 225–240.

1977: 53–62.

Nöllert, A. (1990). Die Knoblauchkröte. A. Ziemsen Verlag, Nussbaum, R. A., and Hinkel, H. (1994). Revision of East Afri-Wittenberg Lutherstadt.

can caecilians of the genera Afrocaecilia Taylor and Boulen-Noonan, B. P. (2000). Does the phylogeny of pelomedusoid gerula Tornier (Amphibia: Gymnophiona: Caeciliaidae).

turtles reflect vicariance due to continental drift? Journal of Copeia 1994: 750–760.

Biogeography 27: 1245–1249.

Nussbaum, R. A., and Tait, C. K. (1977). Aspects of the life his-Noonan, B. P., and Chippindale, P. T. (2006). Vicariant origin of tory and ecology of the Olympic salamander, Rhyacotriton Malagasy reptiles supports late cretaceous antarctic land olympicus

(Gaige).

American

Midland

Naturalist

98:

bridge. American Naturalist 168: 730–741.

176–199.

Norell, M. A. (1989). The higher level relationships of the extant Nussbaum, R. A., and Wilkinson, M. (1989). On the classifica-Crocodylia. Journal of Herpetology 23: 325–335.

tion and phylogeny of caecilians (Amphibia: Gymnophiona). Norell, M. A.

tion and phylogeny of caecilians (Amphibia: Gymnophiona), Norell, M. A., and de Queiroz, K. (1991). The earliest iguanine a critical review. Herpetological Monographs 3: 1–42.

lizard (Reptilia: Squamata) and its bearing on iguanine phy-Nussbaum, R. A., and Wu, S. H. (1995). Distribution, variation, logeny. American Museum Novitates 2997: 1–16.

and systematics of the Seychelles treefrog, Tachycnemis sey-Norell, M. A., and Gao, K. (1997). Braincase and phylogenetic chellensis (Amphibia: Anura: Hyperoliidae). Journal of Zool-relationships of Estesia mongoliensis from the Late Creta-ogy, London 236: 383–406.

ceous of the Gobi Desert and the recognition of a new clade Nussbaum, R. A., and Wu, S. H. (2007). Morphological assess-of lizards. American Museum Novitates 3211: 1–25.

ments and phylogenetic relationships of the Seychellean Norell, M. A., Clark, J.M, and Hutchison, J. H. (1994). The Late frogs of the family Sooglossidae (Amphibia: Anura). Zoolog-Cretaceous alligatoroid Brachychamps Montana [sic] (Cro-ical Studies 46: 322–335.

codylia): New material and putative relationships. American Nussbaum, R. A., Brodie, E. D., Jr., and Storm, R. M. (1983).

Museum Novitates 3116: 1–26.

Amphibians and Reptiles of the Pacific Northwest. University Nores, M. (1999). An alternative hypothesis for the origin of Press Idaho, Moscow, Idaho.

Amazonian bird diversity. Journal of Biogeography 26: Nussbaum, R. A., Jaslow, A., and Watson, J. (1982). Vocaliza-475–485.

tion in frogs of the family Sooglossidae. Journal of Herpetol-Normark, B. B., Judson, O. P., and Moran, N. A. (2003). Geno-ogy 16: 198–204.

mic signatures of ancient asexual lineages. Biological Jour-Nussbaum, R. A., Raxworthy, C. J., Raselimanana, A. P., and nal of the Linnean Society 79: 69–84.

Ramanamanjato, J.-B. (1999). Amphibians and reptiles of Norris, K. S., and Dawson, W. R. (1964). Observations on the the Reserve Naturelle Integrale d’Andohahela, Madagascar.

water economy and electrolyte excretion of chuckwallas Fieldiana Zoology

94: 155–173.

(Lacertilia, Sauromalus). Copeia 1964: 638–646.

Nussbauum, R. A., and Wilkinson, M. (1995). A new genus of Nun˜ez, J. J., and Formas, J. R. (2000). Evolutionary history of lungless tetrapod: A radically divergent caecilian (Amphi-the Chilean frog genus Telmatobufo (Leptodactylidae): an biia: Gymnophiona). Proceedings of the Royal Society B-immunological approach. Amphibia-Reptilia 21: 351–356.

Biological Sciences 261: 331–335.

Nussbaum, R. A. (1976). Geographic variation and systematics Nussear, K. E., Esque, T. C., Haines, D. F., and Tracy, C. R.

of salamanders of the genus Dicamptodon Strauch (Ambysto-

(2007). Desert Tortoise hibernation: Temperatures, timing, matidae). Miscellaneous Publications of the Museum of Zool-and environment. Copeia 2007: 378–386.

ogy, University of Michigan 149: 1–94.

O’Shea, M. (1996). A Guide to the Snakes of Papua New Guinea.

Nussbaum, R. A. (1977). Rhinatrematidae: a new family of cae-Independent Publishing, Port Moresby.

cilians (Amphibia: Gymnophiona). Occasional Papers of the O’Connor, D. E., and Shine, R. (2004). Parental care protects Museum of Zoology, University of Michigan 682: 1–30.

against infanticide in the lizard Egernia saxatilis (Scincidae).

Nussbaum, R. A. (1979). The taxonomic status of the caecilian Animal Behaviour 68: 1361–1369.

genus Uraeotyphlus Peters. Occasional Papers of the Odierna, G., Canapa, A., Andreone, F., Aprea, G., and Barucca, Museum of Zoology, University of Michigan 687: 1–20.

M. (2002). A Phylogenetic Analysis of Cordyliformes Nussbaum, R. A. (1980). Phylogenetic implications of amplectic (Reptilia: Squamata): Comparison of Molecular and Karyo-behavior in sooglossid frogs. Herpetologica 36: 1–5.

logical Data. Molecular Phylogenetics and Evolution 23: Nussbaum, R. A. (1983). The evolution of a unique dual jaw-37–42.

closing mechanism in caecilians (Amphibia: Gymnophiona) Odinchenko, V. I., and Latyshev, V. A. (1996). Keeping and and its bearing on caecilian ancestry. Journal of Zoology, breeding in captivity the Mexican burrowing python Loxoce-London 199: 545–554.

mus bicolor (Cope, 1861) at Moscow Zoo. Russian Journal Nussbaum, R. A. (1984). Amphibians of the Seychelles.

of Herpetology 3: 95–97.

In Biogeography and Ecology of the Seychelles Islands.

Odum, E. P. (1993). Ecology and Our Endangered Life-Support D. R. Stoddart (Ed.). Pp. 378–415. W. Junk, The Hague.

Systems. Sinauer Associates, Inc., Sunderland MA.

Nussbaum, R. A. (1985a). Systematics of caecilians (Amphibia: Oelrich, T. M. (1956). The anatomy of the head of Cteno-Gymnophiona) of the family Scolecomorphidae. Occasional saura pectinata (Iguanidae). Miscellaneous Publications Papers of the Museum of Zoology, University of Michigan of the Museum of Zoology, University of Michigan 94: 713: 1–49.

1–122.

Ohler, A., Grosjean, S., and Hoyos, J. M. (1999). Observation of Oterino, J., Toranzo, G. S., Zelarayan, L., Ajmat, M. T., Bonilla, nest constructing in Taylorana hascheana (Anura: Ranidae).

F., and Buhler, M. I. (2006). Behaviour of the vitelline enve-Revue Francaise d'Aquariologie Herpetologie 26: 67–70.

lope in Bufo arenarum oocytes matured in vitro in blockade Olalla-Tarraga, M. A., and Rodriguez, M. A. (2007). Energy and to polyspermy. Zygote 14: 97–106.

interspecific body size patterns of amphibian faunas in Eur-Ottaviani, G., and Tazzi, A. (1977). The lymphatic system and Tuzzi, A. (1977). The lymphatic system.

ope and North America: anurans follow Bergmann’s rule, In Biology of the Reptilia. Volume 6. Morphology E. C. Gans, urodeles its converse. Global Ecology and Biogeography and T. S. Parsons (Eds.). Pp. 315–462. Academic Press, 16: 606–617.

London.

Oliveira, P. S., and Marquis, R. J. (Eds.) (2002). The Cerrados of Ouboter, P. E., and Nanhoe, L. M. R. (1989). Notes on nesting Brazil: Ecology and Natural History of a Neotropical and parental care in Caiman crocodilus crocodilus in north-Savanna. Columbia University Press, New York.

ern Suriname and an analysis of crocodilian nesting habitats.

Olsson, M., and Madsen, T. (1996). Costs of mating with infer-Amphibia-Reptilia 8: 331–348.

tile males selects for late emergence in females and lizards Overall, K. L. (1994). Lizard egg environments. In Lizard Ecol-

(Lacerta agilis L.). Copeia 1996: 462–464.

ogy: Historical and Experimental Perspectives. L. J. Vitt and Olsson, M., and Madsen, T. (1998). Sexual selection and sperm E. R. Pianka (Eds.). Pp. 51–72. Princeton University Press, competition in reptiles. In Sexual Selection and Sperm Com-Princeton, NJ.

petition. T. Birkhead and A. P. Moller (Eds.). Pp. 503–577.

Packard, G. C., and Kilgore, D. L., Jr. (1968). Internal fertiliza-Academic Press, London.

tion: Adaptive value to early amniotes. Journal of Theoreti-Olsson, M., and Shine, R. (1997). The limits of reproductive out-cal Biology 20: 245–248.

put: Offspring size versus number in the sand lizard (Lacerta Packard, G. C., and Packard, M. J. (1980). Evolution of the clei-agilis). American Naturalist 149: 179–188.

doic egg among reptilian antecedents of birds. American Olsson, M., Madsen, T., and Shine, R. (1997). Is sperm really Zoologist 20: 351–362.

so cheap? Costs of reproduction in male adders, Vipera Packard, G. C., and Packard, M. J. (1988). The physiological berus. Proceedings of the Royal

Society of London B 264: ecology of reptilian eggs and embryos. In Biology of the Rep-455–459.

tilia. Volume 16, B, Defense and Life History. C. Gans and Olsson, M., Shine, R., and Madsen, T. (1996). Sperm selection R. B. Huey (Eds.). Pp. 523–605. Alan R. Liss, Inc, New by females. Nature 383: 585.

York.

Oosterbrock, P. (1987). More appropriate definitions of para-Packard, G. C., Packard, M. J., and Benigan, L. (1991). Sexual phyly and polyphyly, with a comment on the Farris 1974

differentiation, growth, and hatching success by embryonic model. Systematic Zoology 36: 103–108.

painted turtles incubated in wet and dry environments at fluc-Organ, J. A. (1961). Studies of the local distribution, life his-tuation temperatures. Herpetologica 47: 125–132.

tory, and population dynamics of the salamander genus Packard, G. C., Taigen, T. L., Packard, M. J., and Boardman, Desmognathus in Virginia. Ecological Monographs 31: T. J. (1981). Changes in mass of eggs of softshell turtles 189–220.

(Trionyx spiniferus) incubated under hydric conditions simu-Orlov, N. L. (2000). Distribution, comparative morphology and lating those of natural nests. Journal of Zoology, London biology of snakes of Xenopeltis (Serpentes: Macrostomata: 193: 81–90.

Xenopeltidae) in Vietnam. Russian Journal of Herpetology Packard, G. C., Tracy, C. R., and Roth, J. J. (1977). The physio-7: 103–114.

logical ecology of reptilian eggs and embryos, and the evolu-Orlov, N. L. (1997). Viperid snakes (Viperidae Bonaparte, 1840) tion of viviparity within the class Reptilia. Biological of Tam-Dao mountain ridge (Vinh-Phu and Bac-Thai Pro-Reviews 52: 71–105.

vinces, Vietnam). Russian Journal of Herpetology 4: 64–74.

Packard, M. J. (1994). Patterns of mobilization and deposition of Ortega, C. E., Stranc, D. S., Casal, M. P., Hallman, G. M., and calcium in embryos of oviparous, amniotic vertebrates. Israel Muchlinski, A. E. (1991). A positive fever response in Journal of Zoology 40: 481–492.

Agama agama and Sceloporus orcutti (Reptilia, Agamidae Packard, M. J., and DeMarco, V. G. (1991). Eggshell structure and Iguanidae). Journal of Comparatvie Physiology B 161: and formation in eggs of oviparous reptiles. In Egg Incuba-377–381.

tion: Its Effects on Embryonic Development in Birds and Orton, G. L. (1953). The systematics of vertebrate larvae. Sys-Reptiles. D. C. Deeming and M. W. J. Ferguson (Eds.).

tematic Zoology 2: 63–75.

Pp. 53–69. Cambridge University Press, Cambridge.

Osborne, L., and Thompson, M. B. (2005). Chemical composi-Packard, M. J., and Packard, G. C. (1985). Effect of variation in tion and structure of the eggshell of three oviparous lizards.

water-balance of eggs on calcium mobilizaton and growth by Copeia 2005: 683–692.

embryonic painted turtles (Chrysemys picta). American Zool-Ostrom, J. H. (1991). The question of the origin of birds.

ogist 25: A134–A134.

In Origins of the Higher Groups of Tetrapods. Controversy Packard, M. J., and Seymour, R. S. (1997). Evolution of the and Consensus. H.-P. Schultze and L. Trueb (Eds.).

amniote egg. In Amniote Origins. Completing the Transition Pp. 467–484. Comstock Publishing Associates, Ithaca, NY.

to Land. S. S. Sumida and K. L. M. Martin (Eds.).

Ota, H., Honda, M., Kobayashi, M., Sengoku, S., and Hikida, T.

Pp. 265–290. Academic Press, San Diego.

(1999). Phylogenetic relationships of eublepharid geckos Packard, M. J., Packard, G. C., and Boardman, T. J. (1982).

(Reptilia: Squamata): A molecular approach. Zoological Sci-Structure of eggshells and water relations of reptilian eggs.

ence 16: 659–666.

Herpetologica 38: 136–155.

Paladino, F. V., O'Connor, M. P., and Spotila, J. R. (1990).

Parker, H. W. (1934). A Monograph of the Frogs of the Family Metabolism of leatherback turtles, gigantothermy, and ther-Microhylidae. The British Museum, London.

moregulation of dinosaurs. Nature 344: 858.

Parker, M. S. (1994). Feeding ecology of stream-dwelling Pacific Palmer, B. D., Demarco, V., and Guillette, L. J., Jr. (1993). Ovi-giant salamander larvae. (Dicamptodon tenebrosus). Copeia ductal morphology and eggshell formation in the lizard, Sce-1994: 705–718.

loporus woodi. Journal of Morphology 217: 205–217.

Parker, W. S., and Brown, W. S. (1980). Comparative ecology of Palumbi, S. R. (1996). Nucleic acids II: The polymerase chain two colubrid snakes, Masticophis t. taeniatus and Pituophis reaction. In Molecular Systematics, Second Edition. D. M.

melanoleucus deserticola, in northern Utah. Milwaukee Pub-Hillis, C. Moritz, and B. K. Mable (Eds.). Pp. 205–247.

lic Museum, Publications in Biology and Geology 7: 1–104.

Sinauer Associates, Inc., Sunderland, MA.

Parmenter, C. J. (1985). Reproduction and survivorship of Chelo-Panchen, A. L. (1991). The early tetrapods: Classification and dina longicollis (Testudinata: Chelidae). In Biology of Aus-the shape of cladograms. In Origins of the Higher Groups tralasian Frogs and Reptiles. G. Grigg, R. Shine, and H.

of Tetrapods. Controversy and Consensus. H.-P. Schultze Ehmann (Eds.). Pp. 53–61. Surrey Beatty & Sons., Chipping and L. Trueb (Eds.). Pp. 110–144. Comstock Publishing Norton Pty Ltd., Sydney, Australia.

Associates, Ithaca, NY.

Parmenter, C. J., and Heatwole, H. (1975). Panting thresholds of Panchen, A. L., and Smithson, T. R. (1988). The relationships of lizards. 4. Effect of

E., and Simulson, T. R. (1988). The relationships of lizards. 4. Effect of dehydration on panting threshold of the earliest tetrapods. In The Phylogeny and Classification of Amphibolurus barbatus and Amphibolurus muricatus. Jour-the Tetrapods. Vol. 1: Amphibians, Reptiles, Birds. M. J.

nal of Experimental Zoology 191: 327–332.

Benton (Ed.). Pp. 1–32. Clarendon Press, Oxford.

Parmley, D., and Holman, J. A. (1995). Hemphillian (Late Mio-Pang, P. K. T. and Schreibman, M. P. (Eds.). (1986). Vertebrate cene) snakes from Nebraska, with comments on Arikareea Endocrinology: Fundamentals and Biomedical Implications.

through Blancan snakes of midcontinental North America.

Vol. 1. Morphological Considerations. Academic Press, Journal of Vertebrate Paleontology 15: 79–95.

Orlando, FL.

Parra-Olea, G., Garcia-Paris, M., and Wake, D. B. (2004).

Papenfuss, T. J. (1982). The ecology and systematics of the Molecular diversification of salamanders of the tropical amphisbaenian genus Bipes. Occasional Papers of the Cali-American genus Bolitoglossa (Caudata: Plethodontidae) and fornia Academy of Sciences 136: 1–42.

its evolutionary and biogeographical implications. Biological Papenfuss, T. J. (1986). Amphibian and reptile diversity along Journal of the Linnean Society 81: 325–346.

elevational transects in the White-Inyo Range. In Natural Parrish, J. M. (1997). Evolution of the archosaurs. In The Com-History of the White-Inyo Range, Eastern California and plete Dinosaur. J. O. Farlow and M. K. Brett-Surman Western Nevada and High Altitude Physiology. C. A. Hall, (Eds.). Pp. 191–203. Indiana University Press, Bloomington.

Jr., and D. J. Young (Eds.). Pp. 129–136. University of Cali-Parsons, T. S. (1970). The nose and Jacobson’s organ. In Biology fornia White

Mountain

Research

Station Symposium,

of the Reptilia. Volume 2. Morphology B. C. Gans and T. S.

Bishop, CA.

Parsons (Eds.). Pp. 99–191. Academic Press, London.

Parham, J. F., and Fastovsky, D. E. (1998). The phylogeny of Passmore, N., and Carruthers, S. V. (1995). South African Frogs.

cheloniid sea turtles revisited. Chelonian Conservation Biol-A Complete Guide. Revised edition. Southern Books & Wit-ogy [1997]. 2: 548–554.

watersrand University Press, Johannesburg.

Parham, J. F., Feldman, C. R., and Boore, J. L. (2006a). The Patchell, F. C., and Shine, R. (1986a). Feeding mechanisms in complete mitochondrial genome of the enigmatic bigheaded pygopodid lizards: How can Lialis swallow such large prey?

turtle (Platysternon): Description of unusual genomic fea-Journal of Herpetology 20: 59–64.

tures and the reconciliation of phylogenetic hypotheses based Patchell, F. C., and Shine, R. (1986b). Food habitas and repro-on mitochondrial and nuclear DNA. Bmc Evolutionary ductive biology of the Australian legless lizards (Pygopodi-Biology 6.

dae). Copeia 1986: 30–39.

Parham, J. F., Macey, J. R., Papenfuss, T. J., Feldman, C. R., Patten, J. L., da Silva, M. N. F., and Malcolm, J. R. (2000).

Turkozan, O., Polymeni, R., and Boore, J. (2006b). The phy-Mammals of the Rio Juruaánd the evolutionary and ecologi-logeny of Mediterranean tortoises and their close relatives cal diversification of Amazonia. Bulletin of the American based on complete mitochondrial genome sequences from Museum of Natural History 244: 1–306.

museum specimens. Molecular Phylogenetics and Evolution Pauly, G. B., Bernal, X. E., Rand, A. S., and Ryan, M. J. (2006).

38: 50–64.

The vocal sac increases call rate in the tungara frog Physa-Parham, J. F., Simison, W. B., Kozak, K. H., and Feldman, C. R.

laemus pustulosus. Physiological and Biochemical Zoology (2000). A reassessment of some recently described Chinese 79: 708–719.

turtles. American Zoologist 40: 1163.

Pearman, P. B. (1997). Correlates of amphibian diversity in an Parham, J. F., Simison, W. B., Kozak, K. H., Feldman, C. R., and altered landscape of Amazonian Ecuador. Conservation Biol-Shi, H. T. (2001). New Chinese turtles: Endangered or ogy 11: 1211–1225.

invalid? A reassessment of two species using mitochondrial Pearson, O. P. (1977). Effect of substrate and of skin color on DNA, allozyme electrophoresis and known-locality speci-thermoregulation of a lizard. Comparative Biochemistry and mens. Animal Conservation 4: 357–367.

Physiology 58A: 353–358.

Parker, E. D., and Selander, R. K. (1976). The organization of Pearson, O. P., and Bradford, D. F. (1976). Thermoregulation of genetic diversity in the parthenogenetic lizard Cnemido-lizards and toads at high altitudes in Peru. Copeia 1976: phorus tesselatus. Genetics 84: 791–805.

155–169.

Pechmann, J. H. K., and Semlitsch, R. D. (1986). Diel activity Perry, G. (2007). Movement patterns in lizards: Measurement, patterns in the breeding migrations of winter-breeding anur-modality, and behavioral correlates. In Lizard Ecology: The ans. Canadian Journal of Zoology 64: 1116–1120.

Evolutionary Consequences of Foraging Mode. S. M. Reilly, Pechmann, J. H. K., and Wake, D. B. (1997). Declines and disap-L. D. McBrayer, and D. B. Miles (Eds.). Pp. 13–48. Cam-pearances of amphibian populations. In Principles of Conser-bridge University Press, Cambridge, UK.

vation Biology. G. K. Meffe and C. R. Carroll (Eds.).

Perry, G., and Pianka, E. R. (1997). Animal foraging: Past, pres-Pp. 135–137. Sinauer Associates, Inc., Sunderland, MA.

ent, and future. Trends in Ecology & Evolution 12: 360–364.

Pechmann, J. H. K., and Wilbur, H. M. (1994). Putting declining Perry, G., Lampl, I., Lerner, A., Rothenstein, D., Shani, E., amphibian populations in perspective: Natural fluctuations Sivan, N., and Werner, Y. L. (1990). Foraging mode in lacer-and human impacts. Herpetologica 50: 65–84.

tid lizards: Variation and correlates. Amphibia-Reptilia 11: Pechmann, J. H. K., Scott, D. E., Gibbons, J. W., and Semlitsch, 373–384.

R. D. (1989). Influence of wetland hydroperiod on diversity Perry, S. F. (1983). Reptilian lungs. Functional anatomy and evo-and abundance of metamorphosing juvenile amphibians.

lution. Advances in Anatomy, Embryology and Cell Biology Wetlands Ecology and Management 1: 3–11.

29: 1–81.

Pechmann, J. H. K., Scott, D. E., Semlitsch, R. D., Caldwell, Perry, S. F. (1998). Lungs: Comparative anatomy, functional J. P., Vitt, L. J., and Gibbons, J. W. (1991). Declining morphology, and evolution. In Biology of the Reptilia. Vol-amphibian populations: The problem of separating human ume 19, Morphology G. C. Gans and A. S. Gaunt (Eds.).

impacts from natural fluctuations. Science 253: 892–895.

Pp. 1–92. Society for the Study of Amphibians and Reptiles, Pefaur, J. E. (1993). Description of a new Colostethus (Dendro-Ithaca, NY.

batidae) with some natural history comments on the genus Peters, G. (1971). Die intragenerischen Gruppen und die Phylo-in Venezuela. Alytes 11: 88–96.

genese der Schetterlingsagamen (Agamidae: Leiolepis).

Pefaur, J. E., and Duellman, W. E. (1980). Community structure Zoologische Jahrbu¨cher fu¨r Systematik 98: 11–130.

in high Andean herpetofaunas. Transactions of the Kansas Peterson, C. C. (1996). Anhomeostasis: seasonal water and solute Academy of Science 83: 45–65.

relations in two populations of the desert tortoise (Gopherus Pellegrino, K. C. M., Rodrigues, M. T., Yonenaga-Yassuda, Y., agassizii) during chronic drought. Physiological Zoology 69: and Sites, J. J. W. (2001). A molecular perspective on the 1324–1358.

evolution of microteiid lizards (Squamata, Gymnophthalmi-Peterson, C. C., and Stone, P. A. (2000). Physiological capacity dae), and a new classification for the family. Biological Jour-for estivation of the Sonoran Mud Turtle, Kinosternon sonor-nal of the Linnean Society 74: 315–338.

iense. Copeia 2000: 684–700.

Pe´res, A. K., and Colli, G. R. (2004). The taxonomic status of Peterson, C. L., Wilkinson, R. F., Topping, M. S., and Metter, Tupinambis rufescens and T. duseni (Squamata: Teiidae), D. E. (1983). Age and growth of the Ozark hellbender (Cryp-with a redescription of the two species. Occasional Papers tobranchus alleganiensis bishopi). Copeia 1983: 225–231.

of the Sam Noble Oklahoma Museum of Natural History Petranka, J. W. (1998). Salamanders of the United States and 15: 1–12.

Canada. Smithsonian Institute Press, Washington, D.C.

Perez, I., Gimenez, A., Sanchez-Zapata, J. A., Anadon, J. D., Petranka, J. W., Brannon, M. P., Hopey, M. E., and Smith, C. K.

Martinez, M., and Esteve, M. A. (2004). Non-commercial (1994). Effects of timber harvesting on low elevation popula-collection of spur-thighed tortoises (Testudo graeca graeca): tions of southern Applachian salamanders. Forest Ecology A cultural problem in southeast Spain. Biological Conserva-and Management 67: 135–147.

tion 118: 175–181.

Petranka, J. W., Kats, L. B., and Sih, A. (1987). Predator-prey Perez-Higareda, G., Rangel-Rangel, A., Smith, H. M., and interactions among fish and larval amphibians: Use of chem-Chiszar, D. (1989). Comments on the food and feeding habits ical cues to detect predatory fish. Animal Behaviour 35: of Morelet’s crocodile. Copeia 1989: 1039–1041.

420–425.

Pe´rez-Mellado, V., Riera, N., and Perera, A. (Eds.) (2004).

Petren, K., Bolger, D., and Case, T. J. (1993). Mechanisms in the The Biology of Lacertid Lizards: Evolutionary and Eco-competitive success of an invading sexual gecko over an logical Perspectives. Institut Menorquı´ d’Estudis, Mao´, asexual native. Science 259: 354–358.

Menorca.

Petriella, S., Reboreda, J. C., Otero, M., and Segura, E. T.

Pe´rez-Santos, C., and Moreno, A. G. (1991). Serpientes de (1989). Antidiuretic responses to osmotic cutaneous stimula-Ecuador. Museo Regionale di Scienze Naturali – Torino tion in the toad, Bufo arenarum. Journal of Comparative Monografie 11: 1–538.

Physiology 159B: 91–95.

Pergams, O. R. W., and Zaradic, P. A. (2008). Evidence for a Pfennig, D. W., and Murphy, P. J. (2000). Character displace-fundamental and pervasive shift away from nature-based rec-ment in polyphenic tadpoles. Evolution 54: 1738–1749.

reation. Proceedings of the National Academy of Sciences Pfennig, D. W., Harcombe, W. R., and Pfennig, K. S. (2000).

(USA) 105: 2295–2300.

Coral snake mimics are protected only when they occur with Perret, J.- L. (1966). Les amphibiens du Cameroun. Zoologische their model. American Zoologist 40: 1170.

Jahrbu¨cher Abtheelungen Systematik, O¨kologie und Geogra-Pfennig, D. W., Harper, G. R., Brumo, A. F., Harcombe, W. R., phie der Tiere 93: 289–464.

and Pfennig, K. S. (2007). Population differences in preda-Perry, G. (1999). The evolution of search modes: Ecological ver-tion on Batesian mimics in allopatry with their model: Selec-sus phylogenetic perspectives. American Naturalist 153: tion against mimics is strongest when they are common.

98–109.

Behavioral Ecology and Sociobiology 61: 505–511.

Pfingsten, R. A., and Downs, F. L. (Eds.). (1989). Salamanders Pianka, E. R. and King, D. R. (Eds.). (2004). Varanoid Lizards of Ohio. Bulletin of the Ohio Biological Survey 7: 1–315.

of the World. Indiana University Press, Bloomingrton, Indiana.

Phillips, B. L., and Shine, R. (2004). Adapting to an invasive Pianka, E. R., and Parker, W. S. (1975). Ecology of horned species: Toxic cane toads induce morphological change in lizards: A review with special reference to Phrynosoma Australian snakes. Proceedings of the National Academy of platyrhinos. Copeia 1975: 141–162.

Sciences (USA) 101: 17150–17155.

Pianka, E. R., and Vitt, L. J. (2003). Lizards. Windows to the Phillips, B. L., Brown, G. P., Greenlees, M., Webb, J. K., and Evolution of Diversity. University of California Press, Breke-Shine, R. (2007). Rapid expansion of the cane toad (Bufo ley, CA.

marinus) invasion front in tropical Australia. Austral Ecology Pieau, C. (1971). Sur la proportion sexuelle chez les embryons de 32: 169–176.

deux che´loniens (Testudo graeca L. et Emys orbicularis L.) Phillips, B. L., Brown, G. P., Webb, J., and Shine, R. (2006).

issus d'oeufs incubeś artificiellement. Comptes Rendus de Runaway toads: An invasive species evolves speed and thus l'Acade´mie des Sciences, Paris 274: 3071–3074.

spreads more rapidly through Australia. Nature 439: 803.

Pieau, C. (1975). Temperature and sex differentiation in embryos Phillips, J. B., and Borland, S. C. (1994). Use of a specialized of two chelonians, Emys orbicularis L., and Testudo graeca magnetoreception system for homing by the eastern red-L. In Intersexuality in the Animal Kingdom. R. Reinboth spotted newt Notophthalmus viridescens. Journal of Experi-

(Ed.). Pp. 332–339. Springer-Verlag, New York, NY.

mental Biology 188: 275–291.

Piha, H., Pekkonen, M., and Merila, J. (2006). Morphological Phillips, J. B., Deutschlander, M. E., Freake, M. J., and Borland, abnormalities in amphibians in agricultural habitats: A case S. C. (2001). The role of extraocular photoreceptors in newt study of the common frog Rana temporaria. Copeia 2006: magnetic compass orientation: Parallels between light-depen-810–817.

dent magnetoreception and polarized light detection in verte-Pike, D. A. (2006). Movement patterns, habitat use, and growth brates. Journal of

(2006). Movement patterns, habitat use, and growth brates. Journal of Experimental Biology 204: 2543–2552.

of hatchling tortoises, Gopherus polyphemus. Copeia 2006: Phillips, K. (1994). Tracking the Vanishing Frogs. St. Martin's 68–76.

Press, New York.

Pilliod, D. S., Peterson, C. R., and Ritson, P. I. (2002). Seasonal Pianka, E. R. (1966). Convexity, desert lizards and spatial het-migration of Columbia spotted frogs (Rana luteiventris) erogeneity. Ecology 47: 1055–1059.

among complementary resources in a high mountain basin.

Pianka, E. R. (1970). On 'r' and 'K' selection. American Natu-Canadian Journal of Zoology 80: 1849–1862.

ralist 104: 592–597.

Pilorge, T. (1987). Density, size structure, and reproductive char-Pianka, E. R. (1973). The structure of lizard communities.

acteristics of three populations of Lacerta vivipara. Herpeto-Annual Review of Ecology and Systematics 4: 53–74.

logica 43: 345–356.

Pianka, E. R. (1975). Niche relations of desert lizards. In Ecology Pimenta, B. V. S., Haddad, C. F. B., Nascimento, L. B., Cruz, and Evolution of Communities. M. Cody and J. Diamond C. A. G., and Pombal, J. P. (2005). Comment on "Status (Eds.). Pp. 292–314. Harvard University Press, Cambridge, and trends of amphibian declines and extinctions world-Mass.

wide." Science 309: 1999b.

Pianka, E. R. (1985). Some intercontinental comparisons of des-Pimentel, D., Lach, L., Zuniga, R., and Morrison, D. (2000).

ert lizards. National Geographic Research 1: 490–504.

Environmental and economic costs of nonindigenous species Pianka, E. R. (1986). Ecology and Natural History of Desert in the United States. Bioscience 50: 53–65.

Lizards. Analyses of the Ecological Niche and Community Pintak, T. (1987). Zur Kenntnı`s des tomatenfrosches Dyscophus Structure. Princeton University Press. Princeton.

antongili (Erandidier, 1877) (Anura: Microhylidae). Sala-Pianka, E. R. (1988). Evolutionary Ecology. Harper & Row, New mandra 23: 106–121.

York.

Pitman, C. R. S. (1974). A Guide to the Snakes of Uganda.

Pianka, E. R. (1992). The state of the art in community ecology.

Revised Edition. Wheldon & Wesley, Ltd., Codicote, U.K.

In Herpetology: Current Research on the Biology of Amphi-Pitman, N. C. A., Azaldegui, M. D. L., Salas, K., Vigo, G. T., bians and Reptiles. K. Adler (Ed.). Pp. 141–162. Society for and Lutz, D. A. (2007). Written accounts of an Amazonian the Study of Amphibians and Reptiles, Oxford Ohio.

landscape over the last 450 years. Conservation Biology 21: Pianka, E. R. (1994a). Biodiversity of Australian desert lizards.

253–262.

In Biodiversity and Terrestrial Ecosystems. C. I. Peng and Pledge, N. S. (1992). The Curramulka local fauna: A new Late C. H. Chou (Eds.). Pp. 259–281. Institute of Botany, Acade-Tertiary fossil assemblage from Yorke Peninsula, South Aus-mia Sinica Monograph No. 14, Taipei.

tralia. The Beagle 9: 115–142.

Pianka, E. R. (1994b). Comparative ecology of Varanus in the Plummer, M. V. (1976). Some aspects of nesting success in the Great Victoria Desert. Australian Journal of Ecology 19: turtle, Trionyx muticus. Herpetologica 32: 353–359.

395–408.

Plummer, M. V. (1977a). Reproduction and growth in the turtle Pianka, E. R. (1995). Evolution of body size: Varanid lizards as a Trionyx muticus. Copeia 1977: 440–447.

model system. American Naturalist 146: 398–414.

Plummer, M. V. (1977b). Activity, habitat and population struc-Pianka, E. R. (1996). Long-term changes in lizard assemblages in ture in the turtle, Trionyx muticus. Copeia 1977: 431–440.

the Great Victoria Desert: Dynamic habitat mosaics in Plummer, M. V.

the Great Victoria Desert. Dynamic habitat mosaics in Plummer, M. V.
(1985). Growth and maturity in green snakes response to wildfires. In Long-term Studies of Vertebrate (Opheodrys aestivus). Herpetologica 41: 28–33.

Communities. M. L. Cody and J. A. Smallwood (Eds.).

Plummer, M. V. (2004). Seasonal inactivity of the Desert Box Pp. 191–215. Academic Press, San Diego, CA.

Turtle,

Terrapene

ornata

luteola,

at

the

species'

southwestern range limit in Arizona. Journal of Herpetology amphibian extinctions from epidemic disease driven by global 38: 589–593.

warming. Nature 439: 161–167.

Plummer, M. V., and Shirer, H. W. (1975). Movement patterns in Pounds, J. A., Fogden, M. P. L., Savage, J. M., and Gorman, a river population of the softshell turtle, Trionyx muticus.

G. C. (1997). Test of null models for amphibian declines Occasional Papers of the Museum of Natural History, Union a

tropical

mountain.

Conservation

Biology

versity of Kansas 43: 1–26.

1307–1322.

Poe, S. (1997). Data set incongruence and the phylogeny of cro-Poynton, J. C. (1964). The Amphibia of southern Africa: A fau-codilians. Systematic Biology [1996] 45: 393–414.

nal study. Annals of the Natal Museum 17: 1–334.

Poe, S. (1998). Skull characters and the cladistic relationships of Poynton, J. C. (1996). Diversity and conservation of African the Hispaniolan dwarf twig Anolis. Herpetological Mono-bufonids (Anura): Some preliminary findings. African Jour-graphs 12: 192–236.

nal of Herpetology 45: 1–7.

Poe, S. (2004). Phylogeny of anoles. Herpetological Monographs Poynton, J. C., and Broadley, D. G. (1985–1991). Amphibia 18: 37–89.

Zambesiaca. Parts 1–5 Annals of the Natal Museum 26: Poinar, G. R., Jr., and Cannatella, D. C. (1987). An Upper 503–553, 27: 115–181, 28: 161–229, 29: 447–490, 32: Eocene frog from the Dominican Republic and its implica-221–277.

tion for Caribbean biogeography. Science 237: 1215–1216.

Poynton, J. C., and Broadley, D. G. (1987). Amphibia Zambe-Polcyn, M. J., Jacobs, L. L., and Haber, A. (2005). A morpholog-siaca 3. Rhacophoridae and Hyperoliidae. Annals of the ical model and CT assessment of the skull of Pachyrhachis Natal Museum 28: 161–229.

problematicus (Squamata, Serpentes), a 98 million year old Poynton, J. C., and Broadley, D. G. (1988). Amphibia Zambe-snake with legs from the Middle East. Palaeontologia Elec-siaca 4. Bufonidae. Annals of the Natal Museum 29: tronica 8: Article number 26A.

447–490.

Polisar, J. (1996). Reproductive biology of a flood-season nest-Prado, C. P. A., Abdalla, F. C., Silva, A. P. Z., and Zina, J.

ing freshwater turtle of the northern Neotropics: Dermatemys (2004). Late gametogenesis in Leptodactylus labyrinthicus mawii in Belize. Chelonian gametogenesis in Leptodactylus labyrinthicus mawn in Belize. Chelonian Conservation Biology 2: 13–25.

(Amphibia, Anura, Leptodactylidae) and some ecological Pombal, J. P., and Haddad, C. F. B. (1999). Frogs of the genus considerations. Brazilian Journal of Morphological Science Paratelmatobius (Anura: Leptodactylidae) with descriptions 21: 177–184.

of two new species. Copeia 1999: 1014–1026.

Prado, C. P. A., Toledo, L. F., Zina, J., and Haddad, C. F. B.

Pombal, J. P., Jr., Wistuba, E. M., and Bornshein, M. R. (1998).

(2005). Trophic eggs in the foam nests of Leptodactylus A new species of brachycephalid (Anura) from the Atlantic labyrinthicus (Anura, Leptodactylidae): An experimental rain forest of Brazil. Journal of Herpetology 32: 70–74.

approach. Herpetological Journal 15: 279–284.

Pooley, A. C. (1974). Parental care in the Nile crocodile: A pre-Prado, C. P. A., Uetanabaro, M., and Haddad, C. F. B. (2002).

liminary report on behaviour of a captive female. Lammer-Description of a new reproductive mode in Leptodactylus geyer 3: 22–44.

(Anura, Leptodactylidae), with a review of the reproductive Pooley, A. C. (1977). Nest opening response of the Nile croco-specialization toward terrestriality in the genus. Copeia dile Crocodylus niloticus. Journal of Zoology, London 182: 2002: 1128–1133.

17–26.

Pramuk, J. B. (2002). Combined evidence and cladistic relation-Porter, W. P., and Gates, D. M. (1969). Thermodynamic equili-ships of West Indian toads (Anura: Bufonidae). Herpetologi-bria of animals with environment. Ecological Monographs cal Monographs 16: 121–151.

39: 227–244.

Pramuk, J. B. (2006). Phylogeny of South American Bufo Pough, F. H. (1988). Mimicry and related phenomenona.

(Anura: Bufonidae) inferred from combined evidence. Zoo-In Biology of the Reptilia, Vol. 16, Ecology B. Defense and logical Journal of the Linnean Society

146: 407–452.

Life History. C. Gans and R. B. Huey (Eds.). Pp. 153–234.

Pramuk, J. B., Robertson, T., Sites, J. W., and Noonan, B. P.

Alan R. Liss, Inc, New York, NY.

(2008). Around the world in 10 million years: Biogeography Pough, F. H., and Taigen, T. L. (1990). Metabolic correlates of of the nearly cosmopolitan true toads (Anura: Bufonidae).

the foraging and social behaviour of dart-poison frogs. Ani-Global Ecology and Biogeography 17: 72–83.

mal Behaviour 39: 145–155.

Prance, G. T. (1973). Phytogeographic support for the theory of Pough, F. H., and Wilson, R. E. (1977). Acid precipitation and Pleistocene refuges in the Amazon Basin, based on evidence reproductive success of Ambystoma salamanders. Water Air from distributional patterns in Caryocaraceae, Diphapetala-Soil Pollution 7: 307–316.

ceae and Lecythidaceae. Acta Amazonica 3: 5–28.

Pough, F. H., Andrews, R. M., Cadle, J. E., Crump, M. L., Prance, G. T. (1982). A review of the phytogeographic evidences Savitzky, A. H., and Wells, K. D. (1998). Herpetology. Pren-for Pleistocene climate changes in the Neotropics. Annals of tice Hall, Upper Saddle River, NJ.

the Missouri Botanical Garden 69: 594–624.

Pounds, J. A., and Crump, M. L. (1994). Amphibian declines and Prasad, G. V. R., and Rage, J.- C. (1991). A discoglossid frog in climate disturbance: The case of the golden toad and the har-the latest Cretaceous (Maastrichtian) of India. Further evi-lequin frog. Conservation Biology 8: 72–85.

dence for a terrestrial route between India and Laurasia in Pounds, J. A., Bustamante, M. R., Coloma, L. A., Consuegra, J. A., the latest Cretaceous. Comptes Rendus de l’Acade´mie des Fogden, M. P. L., Foster, P. N., La Marca, E., Masters, K. L., Sciences, Paris 313: 273–278.

Merino-Viteri, A., Puschendorf, R., Ron, S. R., Sanchez-Azo-Pregill, G. K., Gauthier, J. A., and Greene, H. W. (1986). The feifa, G. A., Still, C. J., and Young, B. E. (2006). Widespread evolution of helodermatid squamates, with description of a

new taxon and an overview of Varanoidea. Transactions of Biju & Bossuyt (Amphibia: Anura: Nasikabatrachidae) along the San Diego Society of Natural History 21: 167–202.

Western Ghats, with some insights into its bionomics. Cur-Presch, W. (1974). Evolutionary relationships and biogeography rent Science 92: 213–216.

of the macroteiid lizards (Family Teiidae, Subfamily Teii-Radtkey, R. R., Donnellan, S. C., Fisher, R. N., Moritz, C., Han-nae). Bulletin of the Southern California Academy of ley, K. A., and Case, T. J. (1995). When species collide: The Sciences 73: 23–32.

origin and spread of an asexual species of gecko. Proceed-Presch, W. (1988). Phylogenetic relationships of the Scincomor-ings of the Royal Society of London B 259: 145–152.

pha. In Phylogenetic Relationships of the Lizard Families.

Rage, J.-C. (1984). Serpentes. Handbuch der Palaöherpetologie, Essay Commemorating Charles L. Camp. R. Estes and G.

11. Gustav Fischer Verlag, Stuttgart.

Pregill. (Eds.). Pp. 471–492. Stanford University Press, Stan-Rage, J.-C. (1986). Le plus ancien amphibien apode (Gymno-ford, CA.

phiona) fossile. Remarques sur la re´partiition et l’histoire Price, T. D. (1984). The evolution of sexual size dimorphism in paleóbiogeógraphique des gymnophiones. Comptes Rendus Darwin’s finches. American Naturalist 123: 500–518.

de l’Acade´mie des Sciences, Paris 302: 1033–1036.

Pritchard, P. C. H., and Trebbau, P. (1984). The Turtles of Vene-Rage, J.- C. (1987). Fossil history. In Snakes: Ecology and Evolu-zuela. Society for the Study of Amphibians and Reptiles, tionary Biology. R. A. Seigel, J. T. Collins, and S. S. Novak Athens, Ohio.

(Eds.). Pp. 51–76. Macmillian Publ.ishing Co., New York.

Proud, K. R. S. (1978). Some notes on a captive earless monitor Rage, J.-C.

Proud, R. R. S. (1978). Some notes on a captive earless monitor Rage, J.-C. (1996). Les Madsoiidae (Reptilia, Serpentes) du Cre´-

lizard Lanthanotus borneensis. Sarawak Museum Journal 26: taceśupe´rieur d'Europe: Te´moins gondwaniens d'une disper-235–242.

sion transte´thysienne. Comptes Rendus de l'Acade´mie des Pyke, G. H., and Osborne, W. S. (Eds.). (1996). The green & Sciences, Paris, serie II a 322: 603–608.

golden bell frog Litoria aurea: Biology and conservation.

Rage, J. C., and Albino, A. M. (1989). Dinilysia patagonica Australian Zoologist 30: 132–258.

(Reptilia, Serpentes): Materiel vertebral additionel du Cre-Qualls, C. P. (1996). Influence of the evolution of viviparity on tace superieur d'Argentine. Etude complementaire des verte-eggshell morphology in the lizard, Lerista bougainvillii.

bres, variations intraspecifiques et intracolumnaires. Neues Journal of Morphology 228: 119–125.

Jahrbuch fuer Geologie und Palaeontologie Monatshefte Qualls, C. P., and Shine, R. (1995). Maternal body-volume as a 1989: 433–447.

constraint on reproductive output in lizards: Evidence from Rage, J.-C., and Richter, A. (1994). A snake from the Lower Cre-the evolution of viviparity. Oecologia 103: 73–78.

taceous (Barremian) of Spain: The oldest known snake. Nues Quay, W. B. (1972). Integument and the environment: Glandular Jarbuch fu¨r Geologie und Palaöntologie, Monatshefte 1994: composition, function, and evolution. American Zoologist 561–565.

12: 95–108.

Rage, J.-C., and Rocek, Z. (1989). Redescription of Triadobatra-Quay, W. B. (1979). The parietal eye-pineal complex. In Biology of chus massinoti (Piveteau, 1936) an anuran from the Early the Reptilia. Volume 9. Neurology A. C. Gans, R. G. Northcutt, Triassic. Palaeontographica Abteilung A 206: 1–16.

and P. Ulinski (Eds.). Pp. 245–406. Academic Press, London.

Rage, J.-C., Marshall, L. G., and Gayet, M. (1993). Enigmatic Quay, W. B. (1986). Glands. In Biology of the Integument. 2

(1986). Glands. In Biology of the Integument. 2.

Caudata (Amphibia) from the Upper Cretaceous of Gond-Vertebrates. J. Bereiter-Hahn, A. G. Matoltsy, and K. S.

wana. Geobios 26: 515–519.

Richards (Eds.). Pp. 188–193. Springer Verlag, Berlin.

Ragghianti, M., Bucci, S., Marracci, S., Casola, C., Mancino, G., Quinzio, S. I., Fabrezi, M., and Faivovich, J. (2006). Redescrip-Hotz, H., Guex, G. D., Plotner, J., and Uzzell, T. (2007).

tion of the tadpole of Chacophrys pierottii (Vellard, 1948) Gametogenesis of intergroup hybrids of hemiclonal frogs.

(Anura, Ceratophryidae). South American Journal of Herpe-Genetical Research 89: 39–45.

tology 1: 202–209.

Rajendran, M. V. (1985). Studies in Uropeltid Snakes. Publica-Rabb, G. B., and Rabb, M. S. (1960). On the mating and egg-lay-tion Division, Madurai Kamaraj University, Madurai, India.

ing behavior of the Surinam toad, Pipa pipa. Copeia 1960: Ralph, C. L. (1983). Evolution of pineal control of endocrine 271–276.

function in lower vertebrates. American Zoologist 23: Rabb, G. B., and Rabb, M. S. (1963a). Additional observations 597–605.

on breeding behavior of the Surinam toad, Pipa pipa. Copeia Ramı´rez-Bautista, A., Vitt, L. J., Ramı´rez-Hernańdez, A., Qui-1963: 636–642.

jano, F. M., and Smith, G. R. (2008). Reproduction and sex-Rabb, G. B., and Rabb, M. S. (1963b). On the behavior and ual dimorphism of Lepidophyma sylvaticum (Squamata: breeding biology of the African pipid frog Hymenochirus Xantusiidae), a tropical night lizard from Tlanchinol, boettgeri. Zeitschrift fu¨r Tierpsychologie 20: 215–241.

Hidalgo, Mexico. Amphibia-Reptilia 29: 1–10.

Rabb, G. B., and Snediger, R. (1960). Observations on breeding Rand, A. S. (1982). Clutch and egg size in Brazilian iguanid and development of the Surinam toad, Pipa pipa. Copeia lizards. Herpetologica 38: 171–178.

1960: 40–44.

Rand, A. S., Dugan, B. A., Monteza, H., and Vianda, D. (1990).

Radder, R. S., Saidapur, S. K., Shine, R., and Shanbhag, B. A.

The diet of a generalized folivore: Iguana iguana in Panama.

(2006). The language of lizards: Interpreting the function of Journal of Herpetology 24: 211–214.

visual displays of the Indian rock lizard, Psammophilus dor-Rand, W. M., and Rand, A. S. (1976). Agonistic behavior in nest-salis (Agamidae). Journal of Ethology 24: 275–283.

ing iguanas: A stochastic analysis of dispute settlement Radhakrishnan, C., Gopi, K. C., and Palot, M. J. (2007). Exten-dominated by the minimization of energy cost. Zeitschrift sion of range of distribution of Nasikabatrachus sahyadrensis fu¨r Tierpsychologie 40: 279–299.

Ranvestel, A. W., Lips, K. R., Pringle, C. M., Whiles, M. R., DNA sequences: Substitutional bias and information content and Bixby, R. J. (2004). Neotropical tadpoles influence of transitions relative to transversions. Molecular Phyloge-stream benthos: Evidence for the ecological consequences netics and Evolution 4: 203–222.

of decline in amphibian populations. Freshwater Biology Reeder, T. W. (2003). A phylogeny of the Australian Spheno-49: 274–285.

morphus group (Scincidae: Squamata) and the phylogenetic Rao, D.-Q., and Wilkinson, J. A. (2007). A new species of Amo-placement of the crocodile skinks (Trilobonotus): Bayesian lops (Anura: Ranidae) from Southwest China. Copeia 2007: approaches to assessing congruence and obtaining confidence 913–919.

in maximum likelihood inferred relationships. Molecular Rao, D.-Q., and Yang, D.-T. (1992). Phylogenetic systematics of Phylogenetics and Evolution 27: 384–397.

Pareinae (Serpentes) of southeastern Asia and adjacent Reeder, T. W., and Montanucci, R. R. (2001). Phylogenetic anal-islands with relationship between it

Montanucci, R. R. (2001). Phylogenetic anal-islands with relationship between it and the geology change.

ysis of the horned lizards (Phrynosomatidae: Phrynosoma): Acta Zoologica Sinica 38: 139–150.

Evidence from mitochondrial DNA and morphology. Copeia Rao, D.-Q., and Yang, D.-T. (1997). The karyotypes of Mego-2001: 309–323.

phryidae (Pelobatoidea) with a discussion on their classifica-Reeder, T. W., and Wiens, J. J. (1996). Evolution of the lizard tion and phylogenetic relationships. Asiatic Herpetological family Phrynosomatidae as inferred from diverse types of Research 7: 93–102.

data. Herpetological Monographs 10: 43–84.

Rao, D.-Q., Wilkinson, J. A., and Zhang, M. W. (2006). A new Reeder, T. W., Cole, C. J., and Dessauer, H. C. (2002). Phyloge-species of the genus Vibrissaphora (Anura: Megophryidae) netic relationships of whiptail lizards of the genus Cne-from Yunnan Province, China. Herpetologica 62: 90–95.

midophorus (Squamata: Teiidae): A test of monophyly, Ra¨sa¨nen, M. E., Linna, A. M., Santos, J. C. R., and Negri, F. R.

reevaluation of karyotypic evolution, and review of hybrid (1995). Late Miocene tidal deposits in the Amazon foreland origins. American Museum Novitates 3365: 1–61.

basin. Science 269: 386–390.

Reid, K. J. (1955). Reproduction and development in the north-Rashid, S. M. A., and Swingland, I. R. (1998). On the ecology of ern diamondback terrapin, Malaclemys terrapin terrapin.

some freshwater turtles in Bangladesh. In Proceedings: Con-Copeia 1955: 310–311.

servation, Restoration, and Management of Tortoises and Reilly, S. M., and Brandon, R. A. (1994). Partial paedomophosis Turtles – An International Conference [1997]. J. Van in the Mexican stream ambystomatids and the taxonomic sta-Abbema (Ed.). Pp. 224–242. New York Turtle & Tortoise tus of the genus Rhyacosiredon Dunn. Copeia 1994: Society, Purchase, N.Y.

656–662.

Rasmussen, A. R. (1997). Systematics of sea snakes: A critical Reilly, S. M.

Rasmussen, A. R. (1997). Systematics of sea snakes: A critical Reilly, S. M., McBrayer, L. B., and Miles, D. B. (Eds.) (2007a).

review. In Venomous Snakes, Ecology, Evolution and Snake-Lizard Ecology: The Evolutionary Consequences of Foraging bite. R. S. Thorpe, W. Wu¨ster, and A. Malhotra (Eds.).

Mode. Cambridge University Press, Cambridge, MA.

Pp. 15–30. Zoological Society of London, Oxford.

Reilly, S. M., McBrayer, L. D., and Miles, D. B. (2007b). Prey Raup, D. M. (1991). Extinction: Bad Genes or Bad Luck? W. W.

capture and prey processing behavior and the evolution of Norton & Co., New York.

lingual and sensory characteristics: Divergences and conver-Raxworthy, C. J., and Nussbaum, R. A. (1995). Systematics, spe-gences in lizard feeding biology. Lizard Ecology: The Evolu-ciation and biogeography of the dwarf chameleons (Brooke-tionary Consequences of Foraging Mode. S. M. Reilly, L. D.

sia; Reptilia, Squamata, Chamaeleontidae) of northern McBrayer, and D. B. Miles (Eds.). Pp. 302–333. Cambridge Madagascar. Journal of Zoology, London 235: 525–558.

University Press, Cambridge, MA.

Raxworthy, C. J., Forstner, M. R. J., and Nussbaum, R. A.

Reilly, S. M., Wiley, E. O., and Meinhardt, D. J. (1997). An inte-

(2002). Chameleon radiation by oceanic dispersal. Nature grative approach to heterochrony: The distinction between 415: 784–787.

interspecific and intraspecific phenomena. Biological Jour-Raxworthy, C. J., Martinez-Meyer, E., Horning, N., Nussbaum, nal of the Linnean Society 60: 119–143.

R. A., Schneider, G. E., Ortega-Huerta, M. A., and Peterson, Reinert, H. K. (1991). Translocations as a conservation strategy A. T. (2003). Predicting distributions of known and unknown for amphibians and reptiles: Some comments, concerns, and reptile species in Madagascar. Nature 426: 837–841.

observations. Herpetologica 47: 357–363.

Read, K., Keogh, J. S., Scott, I. A. W., Roberts, J. D., and Reisz, R. R., and Laurin, M. (1991). Owenetta and the origin of Doughty, P. (2001). Molecular phylogeny of the Australian turtles. Nature 349: 324–326.

frog genera Crinia, Geocrinia, and allied taxa (Anura: Myo-Reno, H. W., Gehlbach, F. R., and Turner, R. A. (1972). Skin batrachidae). Molecular Phylogenetics and Evolution 21: and aestivational cocoon of the aquatic amphibian, Siren 294–308.

intermedia Le Conte. Copeia 1972: 625–631.

Reagan, D. P. (1991). The response of Anolis lizards to hurri-Rhen, T., and Lang, J. W. (2004). Phenotypic effects of incuba-cane-induced habitat changes in a Puerto Rican rain forest.

tion temperature in reptiles. In Temperature-Dependent Sex Biotropica 23: 468–474.

Determination in Vertebrates. N. Valenzuela and V. Lance Rebouc¸as-Spieker, R., and Vanzolini, P. E. (1978). Parturition in (Eds.). Pp. 91–98. Smithsonian Books, Washington, D. C.

Mabuya macrorhyncha Hoge, 1946 (Sauria, Scincidae), with Riberon, A., Miaud, C., Guyetant, R., and Taberlet, P.

a note on the distribution of maternal behavior in lizards.

(2004). Genetic variation in an endemic salamander, Sal-Papeís Avulsos de Zoologia (Sa˜o Paulo) 32: 95–99.

amandra atra, using amplified fragment length polymor-Reeder, T. W. (1995). Phylogenetic relationships among phryno-phism.

Molecular

Phylogenetics

and

Evolution

31:

somatid lizards as inferred from mitochondrial ribosomal 910–914.

Richards, C. M., and Moore, W. S. (1998). A molecular phyloge-Rocek, Z., and Nessov, L. A. (1993). Cretaceous anurans from netic study of the Old World treefrog family Rhacophoridae.

Central Asia. Palaeontographica Abteilung A 226: 1–54.

Herpetological Journal 8: 41–46.

Rocha, C. F. D. (1990). Reproductive effort in the Brazilian sand Richards, S. J., McDonald, K. R., and Alford, R. A. (1993).

lizard Liolaemus lutzae (Sauria: Iguanidae). Cieˆncia e Cultura Declines in populations of Australia's endemic tropical rain-

(Sa˜o Paulo) 42: 1203–1206.

forest frogs. Pacific Conservation Biology 1: 66–77.

Rocha, C. F. D., and Bergallo, H. G. (1990). Thermal biology Richardson, B. J., Baverstock, P. R., and Adams, M. (1986). Allo-and flight distance of Tropidurus oreadicus (Sauria Iguani-zyme Electrophoresis. A Handbook for Animal Systematics dae) in an area of Amazonian Brazil. Ethology, Ecology & and Population Studies. Academic Press, Sydney.

Evolution 2: 263–268.

Ricklefs, R. E. and Schluter, D. (Eds.). (1994). Species Diversity Rocha, C. F. D., Arau´jo, A. F. B., Vrcibradic, D., and Costa, in Ecological Communities. University of Chicago Press, E. M. M. d. (2000). New Cnemidophorus (Squamata; Teii-Chicago, IL.

dae) from coastal Rio de Janeiro state, southeastner Brazil.

Riemer, W. J. (1957). The snake Farancia abacura: An attended Copeia 2000: 501–509.

nest. Herpetologica 13: 31–32.

Rodda, G. H. (1984). The orientation and navigation of juvenile Rieppel, O. (1988). A review of the origin of snakes. Evolution-alligators: Evidence of magnetic sensitivity. Journal of Com-ary Biology 22: 37–130.

parative Physiology 154A: 649–658.

Rieppel, O. (1993). Euryapsid relationships: A preliminary anal-Rodda, G. H. (1985). Navigation in juvenile alligators. Zeitschrift ysis. Nues Jahrbuch fu¨r Geologie und Palaöntologie, Abhan-fu¨r Tierpsychologie 68: 65–77.

dlungen 188: 241–264.

Rodda, G. H., and Fritts, T. H. (1992). The impact of the intro-Rieppel, O. (1994). The Lepidosauromorpha: An overview with duction of the colubrid snake Boiga irregularis on Guam's special emphasis on the Squamata. In the shadow of the dino-lizards. Journal of Herpetology 26: 166–174.

saurs. Early Mesozoic Tetrapods. N. C. Fraser and H.-D. Sues Rodda, G. H., and Phillips, J. B. (1992). Navigational systems (Eds.). Pp. 23–37. Cambridge University Press, New York.

develop along similar lines in amphibians, reptiles, and birds.

Rieppel, O., and Crumly, C. (1997). Paedomorphosis and skull Ethology, Ecology & Evolution 4: 43–51.

structure in Malagasy chamaeleons (Reptilia: Chamaeleoni-Rodda, G. H., Fritts, T. H., and Campbell, E. W. (1999). The fea-nae). Journal of Zoology, London 243: 351–380.

sibility of controlling the Brown Treesnake in small plots.

Rieppel, O., and deBraga, M. (1996). Turtles as diapsid reptiles.

Problem Snake Management: 468–477.

Nature 384: 453–455.

Rodda, G. H., Fritts, T. H., and McCoid, M. J. (1999). An over-Riley, J., Stimson, A. F., and Winch, J. M. (1985). A review of view of the biology of the Brown Treesnake* (Boiga irregu-Squamata ovipositing in ant and termite nests. Herpetologi-laris), a costly introduced pest on Pacific Islands. In Problem cal Review 16: 38–43.

Snake Management: The Habu and the Brown Treesnake.

Ripa, D. (1999). Keys to understanding the bushmasters (genus G. H. Rodda, Y. Sawai, D. Chizar, and H. Tanaka (Eds.).

Lachesis Daudin, 1803). Bulletin of the Chicago Herpetolog-Pp. 469–477.

Lachesis Daudin, 1803). Bulletin of the Chicago Herpetolog Pp. 465–477. Cornell University Press, Ithaca, NY.

ical Society 34: 45–92.

Rodda, G. H., McCoid, M. J., Fritts, T. H., and Campbell, E. W.

Robb, J. (1986). New Zealand Amphibians and Reptiles In Colour.

(1999). Population trends and limiting factors in Boiga irre-Revised. Collins, Auckland.

gularis. In Problem Snake Management: The Habu and the Roberts, J. D., Horwitz, P., Wardell-Johnson, G., Maxson, L. R., and brown treesnake. G. H. Rodda, Y. Sawai, D. Chiszar, and Mahony, J. (1997). Taxonomy, relationships and conservation of H. Tanaka (Eds.). Pp. 236–253. Cornell University Press, a new genus and species of myobatrachid frog from the high rain-Ithaca, NY.

fall region of southwestern Australia. Copeia 1997: 373–381.

Ro¨del, M. -O., Grafe, T. U., Rudolf, V. H. W., and Ernst, R.

Robertson, A. V., Ramsden, C., Niedzwiecki, J., Fu, J. Z., and (2002). A review of west African spotted Kassina, including Bogart, J. P. (2006). An unexpected recent ancestor of uni-a description of Kassina schioetzi sp nov (Amphibia: Anura: sexual Ambystoma. Molecular Ecology 15: 3339–3351.

Hyperoliidae). Copeia 2002: 800–814.

Robinson, M. D., and Cunningham, A. B. (1978). Comparative Ro¨del, M.-O. (1996). Amphibien der westafrikanischen Savanne.

diet of two Namib Desert sand lizards (Lacertidae). Madoqua Edition Chimaira, Frankfurt am Main.

11: 41–54.

Ro¨del, M.-O. (1998). A reproductive mode so far unknown in Robinson, P. L. (1962). Gliding lizards from the Upper Keuper African

ranids:

Phrynobatrachus

guineensis

Guibe´

&

of Great Britain. Proceedings of the Geological Society of Lamotte, 1961 breeds in tree holes (Anura: Ranidae). Herpe-London 1601: 137–146.

tozoa 11: 19–26.

Rocek, Z. (1994a). A review of the fossil Caudata of Europe.

Ro¨del, M.-O., Spieler, M., Grabow, K., and Bo¨ckheler, C.

Abhandlungen und Berichte fu¨r Naturkunde, Magdeburg (1995). Hemisus marmoratus (Peters, 1854) (Anura: Hemiso-17: 51–56.

tidae),

Fortpflanzungsstrategien

eines

Savannenfrosches.

Rocek, Z. (1994b). Taxonomy and distribution of Tertiary dis-Bonner Zoologische Beitra¨ge 45: 191–207.

coglossids (Anura) of the genus Latonia V. Meyer, 1843.

Rodriguez, L. B., and Cadle, J. E. (1990). A preliminary over-Geobios 27: 717–751.

view of the herpetofauna of Cocha Cashu, Manu National Rocek, Z., and Lamaud, P. (1995). Thaumastosaurus bottii de Park, Peru. In Four Neotropical Rainforests. A. H. Gentry Stefano, 1903, an anuran with Gondwanan affinities from (Ed.). Pp. 410–425. Yale University Press, New Haven, CT.

the Eocene of Europe. Journal of Vertebrate Palaeontology Roelants, K., Gower, D. J., Wilkinson, M., Loader, S. P., Biju, 15: 506–515.

S. D., Guillaume, K., Moriau, L., and Bossuyt, F. (2007).

Global patterns of diversification in the history of modern sulphureus (Wagler) and Spilotes pullatus (Linnaeus). Pro-amphibians. Proceedings of the National Academy of ceedings of the Louisiana Academy of Sciences 29: 152–

156.

Sciences (USA) 104: 887–892.

Rossman, D. A., Ford, N. B., and Seigel, R. A. (Eds.). (1996).

Roelants, K., Jiang, J. P., and Bossuyt, F. (2004). Endemic ranid The Garter Snakes: Evolution and Ecology. University of (Amphibia: Anura) genera in southern mountain ranges of Oklahoma Press, Norman, OK.

the Indian subcontinent represent ancient frog lineages: Evi-Roth, G. (1986). Neural mechanisms of prey recognition: an dence from molecular data. Molecular Phylogenetics and example in amphibians. In Predator-prey Relationships: Per-Evolution 31: 730–740.

spectives and Approaches from the Study of Lower Verte-Rogers, C. L., and Kerstetter, R. E. (1974). The Ecosphere: Organ-brates. M. E. Feder and G. V. Lauder (Eds.). Pp. 42–68.

isms, Habitats, and Disturbances. Harper and Row, New York.

University of Chicago Press, Chicago.

Roman, J., Santhuff, S. D., Moler, P. R., and Bowen, B. W.

Roth, G. (1987). Visual Behavior in Salamanders. Springer-Ver-

(1999). Population structure and cryptic evolutionary units lag, New York.

in the alligator snapping turtle. Conservation Biology 13: Roughgarden, J. (1995). Anolis. Lizards of the Caribbean: Ecol-135–142.

ogy, Evolution, and Plate Tectonics. Oxford University Rome, L. C., Stevens, D. E., and John-Adler, H. B. (1992). The Press, New York.

influence of temperature and thermal acclimation on physio-Rowe, C. L., and Dunson, W. A. (1995). Impacts of hydroperiod on logical function. In Environmental Physiology of the Amphi-growth and survival of larval amphibians in temporary ponds bians. M. E. Feder and W. W. Burggren (Eds.). Pp. 183–205.

of central Pennsylvania, USA. Oecologia 102: 397–403.

University of Chicago Press, Chicago.

Roze, J. A. (1996). Coral Snakes of the Americas: Biology, Iden-Romer, A. S. (1956). Osteology of the Reptiles. University of tification, and Venoms.

Krieger Publishing Company, Mala-Chicago Press, Chicago.

bar, FL.

Romer, A. S. (1960). Vertebrate-bearing continental Triassic Ruben, J. A., Hillenius, W. J., Geist, N. R., Leitch, A., Jones, strata in Mendoza region, Argentina. Geological Society of T. D., Currie, P. J., Horner, J. R., and Espe, G. (1996). The America Bulletin 71: 1279–1293.

metabolic status of some Late Cretaceous dinosaurs. Science Romer, A. S. (1966). Vertebrate Paleontology. (Third Edition).

273: 1204–1207.

University of Chicago Press, Chicago.

Rubio, M. (1998). Rattlesnakes: Protrait of a Predator. Smithso-Ron, S. R., Santos, J. C., and Cannatella, D. C. (2006). Phylog-nian Institute Press, Washington, DC.

eny of the tungara frog genus Engystomops (=Physalaemus Ruby, D. E. (1978). Seasonal changes in the territorial behavior pustulosus species group; Anura: Leptodactylidae). Molecu-of the iguanid lizard, Sceloporus jarrovi. Copeia 1978: lar Phylogenetics and Evolution 39: 392–403.

430–438.

Rose, B. (1982). Lizard home ranges: Methodology and func-Ruby, D. E. (1981). Phenotypic correlates of male reproductive tions. Journal of Herpetology 16: 253–269.

success in the lizard, Sceloporus jarrovi. In Natural Selection Rose, G. J., and Gooler, D. M. (2007). Function of the amphibian and Social Behavior. R. D. Alexander and D. W. Tinkle central auditory system. Hearing and Sound Communication (Eds.). Pp. 96–107. Chiron Press, New York.

in Amphibians 28: 250–290.

Ruby, D. E. (1984). Male breeding success and differential Rose, W. (1962). The Reptiles and Amphibians of Southern access to females in Anolis carolinensis. Herpetologica 40: Africa. Maskew Miller, Ltd., Cape Town, South Africa.

272–280.

Rosenberg, D. K., Noon, B. R., and Meslow, E. C. (1997).

Ruby, D. E., and Dunham, A. E. (1987). Variation in home range Biological corridors, form, function, and efficacy. BioScience size along an elevational gradient in the iguanid lizard Scelo-47: 677–687.

porus merriami. Oecologia 71: 473–480.

Rosenberg, H. I., and Russell, A. P. (1980). Structural and func-Ruby, D. E., and Niblick, H. A. (1994). A behavioral inventory tional aspects of tail squirting: A unique defense mechanism of the desert tortoise: Development of an ethogram. Herpeto-of Diplodactylus (Reptilia: Gekkonidae). Canadian Journal logical Monographs 8: 88–102.

of Zoology 58: 865–881.

Rugh, R. (1951). The Frog. Its Reproduction and Development.

Rosenberg, H. I., Russell, A. P., and Kapoor, M. (1984). Prelimi-McGraw-Hill Book Co, New York.

nary characterization of the defensive secretion of Diplodac-Ruibal, R., and Shoemaker, V. (1984). Osteoderms in anurans.

tylus (Reptilia: Gekkonidae). Copeia 1984: 1025–1028.

Journal of Herpetology 18: 313–328.

Ro¨sler, H. (1995). Geckos der Welt. Alle Gattungen. Urania-Verlag, Ruiz-Carrnaza, P. M., and Lynch, J. D. (1991). Ranas Centrole-Leipzig.

nidae de Colombia. I. Propuesta de una nueva clasificacioń Ross, C. A. (1990). Crocodylus raninus S. Mu¨ller and Schlegel, a gene´rica. Lozania 57: 1–30.

valid species of crocodile (Reptilia: Crocodylidae) from Bor-Runkle, L. S., Wells, K. D., Robb, C. C., and Lance, S. L. (1994).

neo. Proceedings of the Biological Society of Washington Individual, nightly, and seasonal variation in calling behavior 103: 955–961.

of the gray treefrog, Hyla versicolor: Implications for energy Ross, C. A. (Ed.) (1989). Crocodiles and Alligators. Golden expenditure. Behavioral Ecology 5: 318–325.

Press Pty. Ltd, Silverwater, N.S.W.

Russell, A. P. (1988). Limb muscles in relation to lizard system-Rossi, J. V.

Russell, A. P. (1988). Limb muscles in relation to lizard system Rossi, J. V. (1983). The use of olfactory cues by Bufo marinus.

atics: a reappraisal. In Phylogenetic Relationships of the Liz-Journal of Herpetology 17: 72–73.

ard Families. Essay Commemorating Charles L. Camp. R.

Rossman, D. A., and Willliams, K. L. (1966). Defensive behav-Estes and G. Pregill (Eds.). Pp. 493–568. Stanford University ior of the South American colubrid snakes Pseustes Press, Stanford, CA.

Russell, A. P., Bauer, A. M., and Johnson, M. K. (2005). Migra-Saint Girons, H. (1992). Strategies reproductrices des Viperidae tion in amphibians and reptiles: An overview of patterns and dans les zones temperees fraiches et froides. Bulletin de la orientation mechanisms in relation to life history strategies.

Socie´teŹoologique de France 117: 267–278.

In Migration of Organisms: Climate, Geography, Ecology Saint Girons, M.-C. (1970). Morphology of the circulating blood A. M. T Elewa (Ed.). Springer Publishing, New York.

cells. In Biology of the Reptilia. Volume 3. Morphology C. C.

Russell, A. P., and Wu, X.-C. (1997). The Crocodylomorpha at Gans and T. S. Parsons (Eds.). Pp. 73–91. Academic Press, and between geological boundaries: The Baden-Powell London.

approach to change? Zoology 100: 164–182.

Saint, K. M., Austin, C. C., Donnellan, S. C., and Hutchinson, Russell, A. P., Bauer, A. M., and Laroiya, R. (1997). Morpholog-M. N. (1998). C-mos, a nuclear marker useful for squamate ical correlates of the secondarily symmetrical pes of gekko-phylogenetic analysis. Molecular Phylogenetics and Evolu-tan lizards. Journal of Zoology, London 241: 767–790.

tion 10: 259–263.

Ruta, M., and Coates, M. I. (2007). Dates, nodes and character Saint-Aubain,

M. L. de (1985). Blood flow patterns of the respi-conflict: Addressing the lissamphibian origin problem. Jour-ratory systems in larval and adult amphibians: Functional nal of Systematic Palaeontology 5: 67–122.

morphology and phylogenetic significance. Zeitschrift fu¨r Ruta, M., Coates, M. I., and Quicke, D. L. J. (2001). Early tetra-Zoologische Systematik

und

Evolutionsforschung

23:

pod relationships revisited. American Zoologist 41: 1574.

229–240.

Ruta, M., Coates, M. I., and Quicke, D. L. J. (2003). Early tetra-Sakaluk, S. K., and Belwood, J. J. (1984). Gecko phonotaxis to pod relationships revisited. Biological Reviews 78: 251–345.

cricket calling song: A case of satellite predation. Animal Ruta, M., Jeffery, J. E., and Coates, M. I. (2003). A supertree of Behaviour 32: 659–662.

early tetrapods. Proceedings of the Royal Society of London Salemi, M., and Vandamme, A.-M. (2003). The Phylogenetic Series B-Biological Sciences 270: 2507–2516.

Handbook: A Practical Approach to DNA and Protein Ruta, M., Wagner, P. J., and Coates, M. I. (2006). Evolutionary Phylogeny. Sinauer Associates, Sunderland, Mass.

patterns in early tetrapods. I. Rapid initial diversification fol-Salthe, S. N. (1969). Reproductive modes and the numbers and lowed by decrease in rates of character change. Proceedings sizes of ova in the urodeles. American Midland Naturalist of the Royal Society B-Biological Sciences 273: 2107–2111.

81: 467–490.

Ruvinsky, I., and Maxson, L. R. (1996). Phylogenetic relation-Salthe, S. N. (1973a). Amphiuma means Garden. Catalogue of ships among bufonoid frogs (Anura: Neobatrachia) inferred American Amphibians and Reptiles 148: 1–2.

from mitochondrial DNA sequences. Molecular Phyloge-Salthe, S. N.

(1973b). Amphiuma tridactylum Cuvier. Catalogue netics and Evolution 5: 533–547.

of American Amphibians and Reptiles 149: 1–2.

Ryan, M. J. (1985). The Tuńgara Frog. A Study in Sexual Selection Salthe, S. N., and Duellman, W. E. (1973). Quantitative con-and Communication. University of Chicago Press, Chicago.

straints associated with reproductive mode in anurans.

Ryan, M. J., and Rand, A. S. (1995). Female responses to ancestral In Evolutionary Biology of the Anurans. J. L. Vial (Ed.).

advertisement calls in tuńgara frogs. Science 269: 390–392.

Pp. 229–249. University of Missouri Press, Columbia.

Ryan, M. J. (Ed.) (2001). Anuran Communication. Smithsonian Salthe, S. N., and Mecham, J. S. (1974). Reproduction and court-Institution Press, Washington, D. C.

ship patterns. In Physiology of the Amphibia, Volume 2. B.

Ryan, M. J., Tuttle, M. D., and Rand, A. S. (1982). Bat predation Lofts (Ed.). Pp. 309–521. Academic Press, New York.

and sexual advertisment in a Neotropical frog. American Nat-Salvador, A. (1985). Guia de Campo de los Anfibios y Reptiles uralist 119: 136–139.

de la Peninsula Iberica, Islas Baleares y Canarias. Privately Ryan, M. J., Tuttle, M. D., and Taft, L. K. (1981). The costs and printed, Madrid.

benefits of frog chorusing behavior. Behavioral Ecology and Salvador, A., Martıń, J., Lo´pez, P., and Veiga, J. P. (1996).

Sociobiology 8: 273–278.

Long-term effect of tail loss on home-range size and access Ryan, P. (1988). Fiji’s Natural Heritage. Southwestern Publ. Co, to females in male lizards (Psammodromus algirus). Copeia Auckland.

1996: 208–209.

Ryan, T. J., and Semlitsch, R. D. (2003). Growth and the expres-Salvidio, S. (1993). Life history of the European plethodontid sion of alternative life cycles in the salamander Ambystoma salamander Speleomantes ambrosii (Amphibia, Caudata).

talpoideum (Caudata: Ambystomatidae). Biological Journal Herpetological Journal 3: 55–59.

of the Linnean Society 80: 639–646.

San Mauro, D., Gower, D. J., Oommen, O. V., Wilkinson, M., Sabater-Pi, J. (1985). Contribution to the biology of the giant frog and Zardoya, R. (2004). Phylogeny of caecilian amphibians (Conraua goliath, Boulenger). Amphibia-Reptilia 6: 143–153.

(Gymnophiona) based on complete mitochondrial genomes Sage, R. D., Prager, E. M., and Wake, D. B. (1982). A Creta-and nuclear RAG1. Molecular Phylogenetics and Evolution ceous divergence time between pelobatid frogs (Pelobates 33: 413–427.

and Scaphiopus): Immunological studies of serum albumin.

Sanchez-Herraiz, M. J., Barbadillo, L. J., Machordom, A., and Journal of Zoology, London 198: 481–494.

Sanchez, B. (2000). A new species of pelodytid frog from Saint Girons, H. (1970). The pituitary gland. In Biology of the the Iberian Peninsula. Herpetologica 56: 105–118.

Reptilia. Volume 3. Morphology C. C. Gans and T. S. Par-Sanchiz, B., and Rocek, Z. (1996). An overview of the anuran fos-sons (Eds.). Pp. 135–199. Academic Press, London.

sil record. In The Biology of Xenopus. R. C. Tinsley and H. R.

Saint Girons, H. (1988). Les glandes ce´phaliques exocrines des rep-Kobel (Eds.). Pp. 317–328. Zool. Soc. London, London.

tiles. I. Donneés anatomiques et histologiques. Annales des Santos, J. C., Coloma, L. A., and Cannatella, D. C. (2003). Mul-Sciences Naturelles, Zoologie, Paris 13e serie 9: 221–255.

tiple,

recurring

origins

of

aposematism

and

diet

specialization in poison frogs. Proceedings of the National newts (Triturus c. carnifex) at high altitude. Biological Con-Academy of Sciences (USA) 100: 12792–12797.

servation 117: 95–104.

Saporito, R. A., Donnelly, M. A., Hoffman, R. L., Garraffo, H. M., Schaeffel, R., and de Queiroz, A. (1990). Alternative mechan-and Daly, J. W. (2003). A siphonotid millipede (Rhinotus) as isms of enhanced underwater vision in the garter snake the source of spiropyrrolizidine oximes of dendrobatid frogs.

Thamnophis melanogaster and T. couchii. Copeia 1990: Journal of Chemical Ecology 29: 2781–2786.

50–58.

Saporito, R. A., Donnelly, M. A., Norton, R. A., Garraffo, H. M., Schaffner, F. (1998). The liver. In Biology of the Reptilia. Vol-Spande, T. F., and Daly, J. W. (2007). Oribatid mites as a major ume 19, Morphology G. C. Gans and A. S. Gaunt (Eds.).

dietary source for alkaloids in poison frogs. Proceedings of the Pp. 485–531. Society for the Study of Amphibians and Rep-National Academy of Sciences (USA) 104: 8885–8890.

tiles, Ithaca, NY.

Saporito, R. A., Garraffo, H. M., Donnelly, M. A., Edwards, Schall, J. J. (1983). Lizard malaria: Parasite-host ecology. In Lizard A. L., Longino, J. T., and Daly, J. W. (2004). Formicine ants: Ecology. Studies of a Model Organism. R. B. Huey, E. R.

An arthropod source for the pumiliotoxin alkaloids of den-Pianka, and T. W.

Schoener (Eds.). Pp. 84–100. Harvard Uni-drobatid poison frogs. Proceedings of the National Academy versity Press, Cambridge, Mass.

of Sciences (USA) 101: 8045–8050.

Schall, J. J. (1992). Parasite-mediated competition in Anolis Sartorius, S., Vitt, L. J., and Colli, G. R. (1999). Use of naturally lizards. Oecologia 92: 58–64.

and anthropogenically distrurbed habitats in Amazonian rain-Schall, J. J., and Pianka, E. R. (1978). Geographical trends in forest by the teiid lizard Ameiva ameiva. Biological Conser-numbers of species. Science 201: 679–686.

vation 90: 91–101.

Schall, J. J., and Pianka, E. R. (1980). Evolution of escape Saunders, C. D., Brook, A. T., and Myers, O. E. (2006). Using behavior diversity. American Naturalist 115: 551–566.

psychology to save biodiversity and human well-being. Con-Schauinsland, H. (1903). Beitra¨ge zur Entwicklungsgechichte servation Biology 20: 702–705.

und Anatomie der Wirbeltiere. I. Sphenodon, Callorhynchus, Savage, J. M. (1995). Systematics and the biodiversity crisis.

Chama¨leo. Abh. Ges. Zool 39: 1–95.

BioScience 45: 673–679.

Scheltinga, D. M., and Jamieson, B. G. M. (2003a). Spermato-Savage, J. M., and Guyer, C. (1989). Infrageneric classification genesis and the mature spermatozoon: Form function and and species composition of the anole genera, Anolis, Cteno-phylogenetic implications. Reproductive Biology and Phy-notus, Dactyloa, Norops, and Semiurus (Sauria: Iguanidae).

logeny of Anura 2: 119–251.

Amphibia-Reptilia 10: 105–116.

Scheltinga, D. M., and Jamieson, B. G. M. (2003b). The mature Savage, J. M., and Lips, K. R. (1993). A review of the status and spermatozoon. Reproductive Biology and Phylogeny of Uro-biogeography of the lizard genera Celestus and Diploglossus dela 1: 203–274.

(Squamata: Anguidae), with description of two new species Scheltinga, D. M., and Jamieson, B. G. M. (2006). Ultrastructure from Costa Rica. Revista de

Biologıá Tropical 41: 817–842.

and phylogeny of caecilian spermatozoa. In Reproductive Savage, J. M., and Wake, M. H. (2001). Reevaluation of the sta-Biology and Phylogeny of Gymnophiona (Caecilians). J.-M.

tus of taxa of Central American caecilians (Amphibia: Gym-Exbrayat (Ed.). Pp. 247–274. Science Publishers, Enfield, nophiona), with comments on their origin and evolution.

NH.

Copeia 2001: 52–64.

Schiesari, L. C., Grillitsch, B., and Vogl, C. (1996). Comparative Savidge, J. A. (1987). Extinction of an island forest avifauna by morphology of phytotelmonous and pond-dwelling larvae of an introduced snake. Ecology 68: 660–668.

four Neotropical treefrog species (Anura, Hylidae, Osteoce-Savitsky, A. H. (1983). Coadapted character complexes among phalus oophagus, Osteocephalus taurinus, Phrynohyas resi-snakes: Fossoriality, piscivory, and durophagy. American nifictrix, Phrynohyas venulosa). Alytes 13: 109–139.

Zoologist 23: 397–409.

Schiotz, A. (1963). The Amphibia of Nigeria. Videnskabelige Sazima, I. (1991). Caudal luring in two Neotropical pitvipers, Meddelelser fra Dansk naturhistorik Forening 125: 1–92.

Bothrops jararaca and B. jararacussu. Copeia 1991: 245–248.

Schiotz, A. (1967). The treefrogs (Rhacophoridae) of West Sazima, I., and Abe, A. S. (1991). Habits of five Brazilian snakes Africa. Spolia zoologica Musei hauniensis 25: 1–346.

with coral-snake pattern, including a summary of defensive Schiotz, A. (1975). The Treefrogs of East Africa. Steenstrupia, tactics. Studies on Neotropical Fauna and Environment 26: Copenhagen.

159–164.

Schluter, A. (1990). Reproduction and tadpole of Edalorhina Scalia, F. (1976). Structure of the olfactory and accessory perezi (Amphibia, Leptodactylidae). Studies on Neotropical olfactory systems. In Frog

Neurobiology. A Handbook. R.

Fauna and Environment 25: 49–56.

Llinaś and W. Precht (Eds.). Pp. 213–233. Springer-Verlag, Schmalhausen, I. I. (1968). The Origin of Terrestrial Vertebrates.

Berlin.

Academic Press, New York.

Scanlon, J. D. (1992). A new large madtsoiid snake from the Schmitt, M. (1989). Claims and limits of phylogenetic systemat-Miocene of the Northern Territory. The Beagle 9: 49–60.

ics. Zeitschrift fur Zoologische Systematik und Evolutions-Scanlon, J. D., and Lee, M. S. Y. (2004). Phylogeny of Australa-forschung 27: 181–190.

sian venomous snakes (Colubroidea, Elapidae, Hydrophii-Schmitz, A., Brandley, M. C., Mausfeld, P., Vences, M., nae)

based

on

phenotypic

and

molecular

evidence.

Glaw, F., Nussbaum, R. A., and Reeder, T. W. (2005).

Zoologica Scripta 33: 335–366.

Opening the black box: Phylogenetics and morphological Schabetsberger, R., Jehle, R., Maletzky, A., Pesta, J., and Szta-evolution of the malagasy fossorial lizards of the subfam-tecsny, M. (2004). Delineation of terrestrial reserves for ily “Scincinae. Molecular Phylogenetics and Evolution amphibians: Post-breeding migrations of Italian crested 34: 118–133.

Schmuck, R., and Linsemair, K. E. (1988). Adaptations of the year study of home range, movements and population. Mis-reed frog, Hyperolius viridiflavus (Amphibia, Anura, Hyper-souri Department of Conservation Terrestrial series 12: 1–28.

oliidae) to its environment: III. Aspects of nitrogen metabo-Schwenk, K. (1985). Occurrence, distribution and functional sig-lism and osmoregulation in the reed frog, Hyperolius nificance of taste buds in lizards. Copeia 1985: 91–101.

viridiflavus taeniatus, with special reference to the role of iri-Schwenk, K. (1986). Morphology of the tongue in the tuatara, dophores. Oecologia 75: 354–361.

Sphenodon punctatus, (Reptilia: Lepidosauria), with com-Schoener, T. W. (1974). Resource partitioning in ecological ments on function and phylogeny.

(1974). Resource partitioning in ecological nients on function and phylogeny. Journal of Morphology communities. Science 185: 27–38.

188: 129–156.

Schoener, T. W. (1971). Theory of feeding strategies. Annual Schwenk, K. (1988). Comparative morphology of the lepidosaur Review of Ecology and Systematics 2: 369–404.

tongue

and

its

revelance

to

squamate

phylogeny.

Schoener, T. W. (1979). Inferring the properties of predation and In Phylogenetic Relationships of the Lizard Families. Essay other injury-producing agents from injury frequencies. Ecol-Commemorating Charles L. Camp. R. Estes and G. Pregill ogy 60: 1110–1115.

(Eds.). Pp. 569–598. Stanford University Press, Stanford, Schoener, T. W. (1986). Overview: Kinds of ecological commu-CA.

nities—ecology becomes pluralistic. In Community Ecology.

Schwenk, K. (1993). The evolution of chemoreception in squa-J. Diamond and T. J. Case (Eds.). Pp. 467–479. Harper and mate reptiles: A phylogenetic approach. Brain Behavior Row, New York.

and Evolution 41: 124–137.

Schoener, T. W., and Schoener, A. (1982). The ecological correlates Schwenk, K. (1994a). Why snakes have forked tongues. Science of survival in some Bahamian Anolis lizards. Oikos 39: 1–16.

263: 1573–1577.

Schreibman, M. P. (1986). Pituitary gland. In Vertebrate Endocri-Schwenk, K. (1994b). Systematics and subjectivity: The phylog-nology: Fundamentals and Biomedical Implications. Vol. 1.

eny and classification of iguanian lizards revisited. Herpeto-Morphological Considerations. P. K. T. Pang and M. P.

logical Review 25: 53–57.

Schreibman (Eds.). Pp. 11–55. Academic Press, Orlando, FL.

Schwenk, K. (1995). Of tongues and noses: Chemoreception in Schubauer, J. P., Gibbons, J. W., and Spotila, J. R. (1990). Home lizards and snakes. Trends in Ecology and Evolution 10: 7–12.

range and movement patterns of slider turtles inhabiting Par Schwenk, K. (2000). Feeding: Form, Function, and Evolution in Pond. In Life History and Ecology of the Slider Turtle.

Tetrapod Vertebrates. Academic Press, San Diego, CA.

J. W. Gibbons (Ed.). Pp. 223–232. Smithsonian Institution Schwenk, K., and Greene, H. W. (1987). Water collection and Press, Washington.

drinking in Phrynocephalus helioscopus: A possible conden-Schulte, J. A., Losos, J., Cruz, F. B., and Nun˜ez, H. (2004). The sation mechanism. Journal of Herpetology 21: 134–139.

relationship between morphology, escape behavior and Schwenk, K. (Ed.) (2000). Feeding, Form, Function, and microhabitat occupation in the lizard clade Liolaemus (Igua-Evolution in Tetrapod Vertebrates. Academic Press, San nidae: Tropidurinae: Liolaemini). Journal of Evolutionary Diego, CA.

Biology 17: 408–420.

Scott, A. C. (1980). The ecology of some Upper Palaeozoic Schulte, J. A., II., Macey, J. R., Espinoza, R. E., and Larson, A.

floras. In The Terrestrial Environment and the Origin of (2000). Phylogenetic relationships in the iguanid lizard genus Land Vertebrates. A. L. Panchen (Ed.). Pp. 87–115. Aca-Liolaemus: Multiple origins of viviparous reproduction and demic Press, London.

evidence for recurring Andean vicariance and dispersal.

Scott, D. E. (1990). Effects of larval density in Ambystoma opa-Biological Journal of the Linnean Society 69: 75–102.

cum: an experiment in large-scale field enclosures. Ecology Schulte, J. A., Valladares, J. P., and Larson, A. (2003). Phyloge-71: 296–306.

netic relationships within iguanidae inferred using molecular Scott, D. E. (1994). The effect of larval density on adult demo-and morphological data and a phylogenetic taxonomy of graphic traits in Ambystoma opacum. Ecology 75: 1383–1396.

iguanian lizards. Herpetologica 59: 399–419.

Scott, E. (2005). A phylogeny of ranid frogs (Anura: Ranoidea: Schultz, J. (2005). The Ecozones of the World. (2nd Ed.).

Ranidae), based on a simultaneous analysis of morphological Springer, Berlin.

and molecular data. Cladistics 21: 507–574.

Schultze, H.-P. (1991). A comparison of controversial hypoth-Scott, I. A. W., Keogh, J. S., and Whiting, M. J. (2004). Shifting eses on the origin of tetrapods. In Origins of the Higher sands and shifty lizards: molecular phylogeny and biogeogra-Groups of Tetrapods. Controversy and Consensus. H.-P.

phy of African flat lizards (Platysaurus). Molecular Phyloge-Schultze and L. Trueb (Eds.). Pp. 29–67. Comstock Publish-netics and Evolution 31: 618–629.

ing Associates, Ithaca, NY.

Scott, N. J., Jr. (1976). The abundance and diversity of the herpe-Schultze, H.-P. (1994). Comparison of hypotheses on the relation-tofaunas of tropical forest litter. Biotropica 8: 41–58.

ships of sarcopterygians. Systematic Biology 43: 155–173.

Seben, K. P. (1987). The ecology of indeterminate growth in ani-Schultze, H.-P. and Trueb, L. (Eds.) (1991). Origins of the mals. Annual Review of Ecology and Systematics 18: Higher Groups of Tetrapods. Controversy and Consensus.

371–407.

Comstock Publishing Associates, Ithaca, NY.

Secor, S. M. (1994). Ecological significance of movements and Schwartz, A., and Henderson, R. W. (1991). Amphibians and activity range for the sidewinder, Crotalus cerastes. Copeia Reptiles of the West Indies: Descriptions, Distributions. and 1994: 631–645.

Natural History. University of Florida Press, Gainesville, FL.

Secor, S. M., and Nagy, K. A. (1994). Bioenergetic correlates of Schwartz, E. R., Schwartz, C. W., and Kiester, A. R. (1984). The foraging for the snakes Crotalus cerastes and Masticophis three-toed box turtle in central Missouri, part II: a nineteen-flagellum. Ecology 75: 1600–1614.

Secor, S. M., Jayne, B. C., and Bennett, A. F. (1992). Locomotor Semlitsch, R. D. (1987). Relationship of pond drying to the performance and energetic cost of sidewinding by the snake reproductive success of the salamander Ambystoma talpoi-Crotalus cerastes. Journal of Experimental Biology 163: 1–14.

deum. Copeia 1987: 61–69.

Seddon, J. M., Baverstock, P. R., and Georges, A. (1998). The Semlitsch, R. D. (1998). Biological delineation of terrestrial rate of mitochondrial 12S rRNA gene evolution is similar buffer zones for pond-breeding salamanders. Conservation in freshwater turtles and marsupials. Journal of Molecular Biology 12: 1113–1119.

Evolution 46: 460–464.

Semlitsch, R. D., and Gibbons, J. W. (1988). Fish predation in Seddon, J. M., Georges, A., Baverstock, P. R., and McCord, W.

size-structured populations of treefrog tadpoles. Oecologia (1997). Phylogenetic relationships of chelid turtles (Pleuro-75: 321–326.

dira: Chelidae) based on mitochondrial 12S rRNA gene Semlitsch, R. D., Scott, D. E., and Pechmann, J. H. K. (1988).

sequence variation. Molecular Phylogenetics and Evolution Time and size at metamorphosis related to adult fitness in 7: 55–61.

Ambystoma talpoideum. Ecology 69: 184–192.

Seebacher, F., and Shine, R. (2004). Evaluating thermoregulation Semlitsch, R. D., Scott, D. E., Pechmann, J. H. K., and Gibbons, in reptiles: The fallacy of the inappropriately applied method.

J. W. (1996). Structure and dynamics of an amphibian com-Physiological and Biochemical Zoology 77: 688–695.

munity: Evidence from a 16–year study of a natural pond.

Seigel, R. A. (1983). Natural survival of eggs and tadpoles of the In Long-term Studies of Vertebrate Communities. M. L. Cody wood frog, Rana sylvatica. Copeia 1983: 1096–1098.

and J. A. Smallwood (Eds.). Pp. 217–248. Academic Press, Seigel, R. A. and Collins, J. T. (Eds.) (1993). Snakes: Ecology San Diego.

and Behavior. McGraw-Hill, Inc, New York.

Semple, C., and Steel, M. (2003). Phylogenetics. Oxford Lecture Seigel, R. A. and Collins, J. T. (Eds.) (2002). Snakes: Ecology Series in Mathematics and Its Applications, Oxford Univer-and Behavior. McGraw-Hill, Inc, New York.

sity Press, Oxford, UK.

Seigel, R. A., and Ford, N. B. (1991). Phenotypic plasticity in the Sessions, S. K. (1996). Chromosomes: Molecular cytogenetics.

reproductive characteristics of an oviparous snake, Elaphe In Molecular Systematics, Second Edition. D. M. Hillis, guttata: Implications for life history studies. Herpetologica C. Moritz, and B. K. Mable (Eds.). Pp. 121–168. Sinauer 47: 301–307.

Associates, Inc., Sunderland, Mass.

Seigel, R. A., and Ford, N. B. (1987). Reproductive ecology.

Sessions, S. K., and Ruth, S. B. (1990). Explanation for naturally In Snakes: Ecology and Evolutionary Biology. R. Seigel, occurring supernumerary limbs in amphibians. Journal of J. T. Collins, and S. S. Novak (Eds.). Pp. 210–252. Macmil-Experimental Zoology 254: 38–47.

lan Publishing Company, New York, NY.

Sever, D. M. (1991a). Comparative anatomy and phylogeny of Seigel, R. A., Fitch, H. S., and Ford, N. B. (1986). Variation in the cloacae of salamanders (Amphibia: Caudata). I. Evolu-relative clutch mass on snakes among and within species.

tion at the family level. Herpetologica 47: 165–193.

Herpetologica 42: 179–185.

Sever, D. M. (1991b). Comparative anatomy and phylogeny of Seigel, R. A., Huggins, M. M., and Ford, N. B. (1987). Reduction the cloacae of salamanders (Amphibia: Caudata). II. Crypto-in locomotor ability as a cost of reproduction in gravid branchidae, Hynobiidae, and Sirenidae. Journal of Morphol-snakes. Oecologia 73: 481–485.

ogy 207: 283–301.

Seigel, R. A., Loraine, R. K., and Gibbons, J. W. (1995). Repro-Sever, D. M. (1992). Comparative anatomy and phylogeny of the ductive cycles and temporal variation in fecundity in the cloacae of salamanders (Amphibia: Caudata). VI. Ambysto-black swamp snake, Seminatrix pygaea. American Midland matidae and Dicamptodontidae. Journal of Morphology Naturalist 134: 371–377.

212: 305–322.

Seigel, R. A., Smith, R. B., Demuth, J., Ehrhart, L. M., and Snel-Sever, D. M. (1994). Observations on regionalization of secre-son, F. F. (2002). Amphibians and reptiles of the John F.

tory activity in the spermathecae of salamanders and com-Kennedy Space Center, Florida: A long-term assessment of ments

on

phylogeny

of

sperm

storage

in

female

a large protected habitat (1975–2000). Florida Scientist 65: amphibians. Herpetologica 50: 383–397.

1–12.

Sever, D. M. (2003). Courtship and mating glands. Reproductive Selcer, K. W. (1990). Egg-size relationships in a lizard with Biology and Phylogeny of Urodela 1: 323–381.

fixed clutch size: Variation in a population of the Mediterra-Sever, D. M. (Ed.) (2003). Reproductive Biology and Phylogeny nean gecko. Herpetologica 46: 15–21.

of Anura. Volume 2 of the series Reproductive Biology and Semlitsch, R. D. (1980). Geographic and local variation in popu-Phylogeny, series Editor, B. G. M. Jamieson. Science publation parameters of the slimy salamander Plethodon glutino-lishers, Inc., Enfield, NH, USA.

sus. Herpetologica 36: 6–16.

Sever, D. M., and Kloepeer, N. M. (1993). Spermathecal cytol-Semlitsch, R. D. (1981). Effects of implanted tantalum-182 wire ogy of Ambystoma opacum (Amphibia: Ambystomatidae) tags on the mole salamander, Ambystoma talpoideum. Copeia and the phylogeny of sperm storage organs in female sala-1981: 735–737.

manders. Journal of Morphology 217: 114–127.

Semlitsch, R. D. (1985a). Analysis of climatic factors influen-Sever, D. M., Heinz, E. A., Lempart, P. A., and Taghon, M. S.

cing migrations of the salamander Ambystoma talpoideum.

(1990). Phylogenetic significance of the cloacal anatomy of Copeia 1985: 477–489.

female bolitoglossine salamanders (Plethodontidae, tribe Semlitsch, R. D. (1985b). Reproductive strategy of a faculta-Bolitoglossini). Herpetologica 46: 431–446.

tively paedomorphic salamander Ambystoma talpoideum.

Sever, D. M., Rania, L. C., and Krenz, J. D. (1996a). Annual cycle Oecologia 65: 305–313.

of sperm storage in spermathecae of the red-spotted newt,

Notophthalmus

viridescens

(Amphibia:

Salamandridae).

Sherbrooke, W. C. (1981). Horned Lizards. Unique Reptiles of Journal of Morphology 227: 155–170.

Western North America. Southwestern Parks & Monument Sever, D. M., Rania, L. C., and Krenz, J. D. (1996b). Reproduc-Association, Globe, AZ.

tion of the salamander Siren intermedia Le Conte with espe-Sherbrooke, W. C. (1990). Rain-harvesting in the lizard, Phryno-cial reference to oviducal anatomy and mode of fertilization.

soma cornutum: Behavior and integumental morphology.

Journal of Morphology 227: 335–348.

Journal of Herpetology 24: 302–308.

Sexton, O. J. (1959). Spatial and temporal movements of a pop-Sherbrooke, W. C., and Montanucci, R. R. (1988). Stone mimicry in ulation of the painted turtle Chrysemys picta marginata the round-tailed horned lizard, Phrynosoma modestum (Sauria: (Agassiz). Ecological Monographs 29: 113–140.

Iguanidae). Journal of Arid Environments 14: 275–284.

Sexton, O. J., Ortleb, E. P., Hathaway, L. M., and Ballinger, R. E.

Sherbrooke, W. C., Scardino, A. J., de Nys, R., and Schwarz-

(1971). Reproductive cycles of three species of anoline lizards kopf, L. (2007). Functional morphology of scale hinges used from the Isthmus of Panama. Ecology 52: 201–215.

to transport water: Convergent drinking adaptations in desert Seymour, R. S. (1982). Physiological adaptations to aquatic life.

lizards (Moloch horridus and Phrynosoma cornutum). Zoo-Biology of Reptilia 13: 1–51.

morphology 126: 89–102.

Seymour, R. S., and Bradford, D. F. (1995). Respiration of Shi, H. T., and Parham, J. F. (2001). Preliminary observations of amphibian eggs. Physiological Zoology 68: 1–25.

a large turtle farm in Hainan Province, People's Republic of Shaffer, H. B.

a large turtle farm in Hainan Province, People's Republic of Shaffer, H. B. (1993). Phylogenetics of model organisms: the China. Turtle and Tortoise Newsletter 3: 4–6.

laboratory axolotl, Ambystoma mexicanum. Systematic Biol-Shi, H. T., Parham, J. F., Lau, M., and Tien-Hsi, C. (2007).

ogy 42: 508–522.

Farming endangered turtles to extinction in China. Conserva-Shaffer, H. B., and McKnight, M. L. (1996). The polytypic tion Biology 21: 5–6.

species revisited: Genetic differentiation and molecular Shi, H., Fan, Z., Yin, F., and Yuan, Z. (2004). New data on the phylogenetics of the tiger salamander Ambystoma tigrinum trade and captive breeding of turtles in Guangxi Province, (Amphibia: Caudata) complex. Evolution 50: 417–433.

south China. Asiatic Herpetological Research 10: 126–128.

Shaffer, H. B., Meylan, P., and McKnight, M. L. (1997). Tests of Shine, R. (1978). Sexual size dimorphism and male combat in turtle phylogeny: molecular, morphological, and paleontolog-snakes. Oecologia 33: 269–277.

ical approaches. Systematic Biology 46: 235–268.

Shine, R. (1979). Sexual selection and sexual dimorphism in the Shaffer, H. B., Clark, J. M., and Kraus, F. (1991). When mole-Amphibia. Copeia 1979: 297–306.

cules and morphology clash: A phylogenetic analysis of the Shine, R. (1980a). Ecology of the Australian death adder North

American

ambystomatid

salamanders

(Caudata:

Acanthophis antarcticus (Elapidae): Evidence for conver-Ambystomatidae). Systematic Zoology 40: 284–303.

gence with the Viperidae. Herpetologica 36: 281–289.

Shaffer, M. L. (1981). Minimum population sizes for species Shine, R. (1980b). Costs" of reproduction in reptiles. Oecologia conservation. BioScience 31: 131–134.

31: 131–134.

46: 92–100.

Shah, B., Shine, R., Hudson, S., and Kearney, M. (2003). Social-Shine, R. (1980c). Reproduction, feeding and growth in the Aus-ity in lizards: Why do thick-tailed geckos (Nephrurus milii) tralian burrowing snake Vermicella annulata. Journal of Her-aggregate? Behaviour 140: 1039–1052.

petology 14: 71–77.

Shaldybin, S. L. (1981). Wintering and number of amphibians and Shine, R. (1983). Reptilian viviparity in cold climates: Testing reptiles of Lazo State Nature Reserve. In Herpetological Inves-the assumptions of an evolutionary hypothesis. Oecologia tigations in Siberia and the Far East. L. J. Borkin (Ed.).

57: 397–405.

Pp. 123–124. Academy of Science USSR, Zoology Institute, Shine, R. (1985a). The reproductive biology of Australian reptiles: Leningrad.

a search for general patterns. In Biology of Australasian Frogs Shea, G. M. (1993). Family Pygopodidae. In Fauna of Australia.

and Reptiles. G. Grigg, R. Shine, and H. Ehmann (Eds.).

Volume 2A. Amphibia & Reptilia. C. J. Gasby, G. J. B. Ross, Pp. 297–303. Surrey Beatty & Sons Pty Ltd., Chipping Norton and P. L. Beesley (Eds.). Pp. 234–239. Australian Govern-Pty Ltd., Sydney, Australia.

ment Publishing Service, Canberra.

Shine, R. (1985b). The evolution of viviparity in reptiles: an eco-Shea, G., Shine, R., and Covacevich, J. C. (1993). Family Elapidae.

logical analysis. In Biology of the Reptilia. Volume 15, In Fauna of Australia. Volume 2A. Amphibia & Reptilia. C. J.

Developmental Biology B. C. Gans and F. Billett (Eds.).

Gasby, G. J. B. Ross, and P. L. Beesley (Eds.). Pp. 295–309.

Pp. 677–680. John Wiley & Sons, Inc, New York.

Australian Government Publishing Service, Canberra.

Shine, R. (1986a). Ecology of a low-energy specialist: Food Sheil, C. A. (1999). Osteology and skeletal development of Pyx-habits and reproductive biology of the Arafura filesnake icephalus adspersus (Anura: Ranidae: Raninae). Journal of (Acrochordidae). Copeia 1986: 424–437.

Morphology 240: 49–75.

Shine, R. (1986b). Sexual differences in morphology and niche Sheil, C. A., and Mendelson, J. R. (2001). A new species of utilization in an aquatic snake, Acrochordus arafurae. Oeco-Hemiphractus (Anura: Hylidae: Hemiphractinae), and a rede-logia 69: 260–267.

scription of H. johnsoni. Herpetologica 57: 189–202.

Shine, R. (1987). The evolution of viviparity: Ecological corre-Sheldahl, L. A., and Martins, E. P. (2000). The territorial behav-lates of reproductive mode within a genus of Australian ior of the western fence lizard, Sceloporus occidentalis. Her-snakes (Pseudechis: Elapidae). Copeia 1987: 551–563.

petologica 56: 469–479.

Shine, R. (1988). Parental care in reptiles. In Biology of the Rep-Shepard, D. B., and Caldwell, J. P. (2005). From foam to free-tilia, Vol. 16, Ecology B. Defense and Life History. C. Gans living: Ecology of larval Leptodactylus labyrinthicus. Copeia and R. D. Huey (Eds.). Pp. 275–329. Alan R. Liss, Inc., 2005: 803–811.

New York.

Shine, R. (1991a). Intersexual dietary divergence and the evolu-oviparous reptiles from reproducing at high elevations.

tion of sexual dimorphism in snakes. American Naturalist Biological Journal of the Linnean Society 78: 325–334.

138: 103–122.

Shine, R., Elphick, M. J., and Harlow, P. S. (1997a). The influ-Shine, R. (1991b). Australian Snakes. A Natural History. Cornell ence of natural incubation environments on the phenotypic University Press, Ithaca, N.Y.

traits of hatchling lizards. Ecology 78: 2559–2568.

Shine, R. (1994). Sexual dimorphism in snakes revisited. Copeia Shine, R., Haagner, G. V., Branch, W. R., Harlow, P. S., and 1994: 326–346.

Webb, J. K. (1996b). Natural history of the African shield-Shine, R. (2002). An empirical test of the ‘predictability’ hypoth-nose snake Aspididelaps scutatus (Serpentes, Elapidae).

esis for the evolution of vivipariity in reptiles. Journal of Journal of Herpetology 30: 361–366.

Evolutionary Biology 15: 553–560.

Shine, R., Harlow, P. S., and Keogh, J. S. (1996e). Commercial Shine, R. (2003a). Locomotor speeds of gravid lizards: Placing harvesting of giant lizards: The biology of water monitors ‘costs of reproduction’ within an ecological context. Func-Varanus salvator in southern Sumatra. Biological Conserva-tional Ecology 17: 526–533.

tion 77: 125–134.

Shine, R. (2003b). Reproductive strategies in snakes. Proceed-Shine, R., Harlow, P. S., Branch, W. R., and Webb, J. K.

ings of the Royal Society of London B 270: 995–1004.

(1996c). Life on the lowest branch: Sexual dimorphism, Shine, R. (2004). Seasonal shifts in nest temperature can modify diet, and reproductive biology of an African twig snake, the phenotypes of hatchling lizards, regardless of overall Thelotornis

capensis

(Serpentes,

Colubridae).

Copeia

mean incubation temperature. Functional Ecology 18: 43–49.

1996: 290–299.

Shine, R. (2005). Life-history evolution in reptiles. Annual Shine, R., Langkilde, T., and Mason, R. T. (2004a). Courtship Review of Ecology Evolution and Systematics 36: 23–46.

tactics in garter snakes: How do a male’s morphology and Shine, R., and

Bull, J. J. (1979). The evolution of life-bearing in behavior influence his mating success? Animal Behaviour lizards and snakes. American Naturalist 113: 905–923.

67: 477–483.

Shine, R., and Fitzgerald, M. (1996). Large snakes in a mosaic Shine, R., Langkilde, T., Wall, M. D., and Mason, R. T. (2005b).

rural landscape: The ecology of carpet pythons Morelia spi-Alternative male mating tactics in garter snakes. Animal lota (Serpentes: Pythonidae) in coastal eastern Australia.

Behaviour 70: 387–396.

Biological Conservation 76: 113–122.

Shine, R., Madsen, T. R. L., Elphick, M. J., and Harlow, P. S.

Shine, R., and Harlow, P. S. (1996). Maternal manipulation of (1997). The influence of nest temperatures and maternal offspring phenotypes via nest-site selection in an oviparous brooding on hatchling phenotypes of water pythons. Ecology lizard. Ecology 77: 1808–1817.

78: 1713–1721.

Shine, R., and Houston, D. (1993). Family Acrochordidae. In Fauna Shine, R., O’Connor, D., LeMaster, M. P., and Mason, R. T.

of Australia. Volume 2A. Amphibia & Reptilia. C. J. Gasby, (2001a). Pick on someone your own size: Ontogenetic shifts G. J. B. Ross, and P. L. Beesley (Eds.). Pp. 322–324. Australian in mate choice by male garter snakes result in size-assortative Government Publishing Service, Canberra.

mating. Animal Behaviour 61: 1133–1141.

Shine, R., and Lambeck, R. (1985). A radiotelemetric study of Shine, R., O’Connor, D., and Mason, R. T. (2000a). Female movements, thermoregulation and habitat utilization of Ara-mimicry in garter snakes: Behavioural tactics of “she-males”

fura filesnakes (Serpentes: Acrochordidae). Herpetologica and the males that court them. Canadian Journal of Zoology 41: 351–361.

78: 1391–1396.

Shine, R., and Mason, R. T. (2005). Does large body size in Shine, R., O’Connor, D., and Mason, R. T. (2000b). Sexual con-males evolve to facilitate forcible insemination? A study on flict in the snake den. Behavioral Ecology and Sociobiology garter snakes. Evolution 59: 2426–2432.

48: 392–401.

Shine, R., and Olsson, M. (2003). When to be born? Prolonged Shine, R., O’Donnell, R. P., Langkilde, T., Wall, M. D., and pregnancy or incubation enhances locomotor performance Mason, R. T. (2005a). Snakes in search of sex: The relation-in neonatal lizards (Scincidae). Journal of Evolutionary Biol-ship between mate-locating ability and mating success in ogy 16: 823–832.

male garter snakes. Animal Behaviour 69: 1251–1258.

Shine, R., and Schwaner, T. (1985). Prey constriction by venom-Shine, R., Phillips, B., Langkilde, T., Lutterschmidt, D., Waye, ous snakes: A review, and new data on Australian species.

H., and Mason, R. T. (2004b). Mechanisms and conse-Copeia 1985: 1067–1071.

quences of sexual conflict in garter snakes (Thamnophis sir-Shine, R., and Schwarzkopf, L. (1992). The evolution of repro-talis, Colubridae). Behavioral Ecology 15: 654–660.

ductive effort in lizards and snakes. Evolution 46: 62–75.

Shine, R., Phillips, B., Waye, H., LeMaster, M., and Mason, Shine, R., and Slip, D. J. (1990). Biological aspects of the adap-R. T. (2001b). Advantage of female mimicry to snakes.

tive radiation of Australasian pythons (Serpentes: Boidae).

Nature 414: 267.

Herpetologica 46: 283–290.

Shine, R., Schwarzkopf, L., and Caley, M. J. (1996d). Energy, Shine, R., Branch, W. R., Harlow, P. S., and Webb, J. K.

risk, and reptilian reproductive effort: A reply to Niewiar-

(1996a). Sexual dimorphism, reproductive biology, and food owski and Dunham. Evolution. 50: 2111–2114.

habits of two species of African file snakes (Mehelya: Colu-Shine, R., S habits of two species of African filesnakes (Mehelya, Colu-Shine, R., Sun, L., Fitzgerald, M., and Kearney, M. 2002. Behav-bridae). Journal of Zoology, London 240: 327–340.

ioral responses of free-ranging pit-vipers (Gloydius she-Shine, R., Elphick, M. J., and Barrott, E. G. (2003). Sunny side daoensis, Viperidae) to approach by a human. Copeia up: Lethally high, not low, nest temperatures may prevent 2002: 834–850.

Shine, R., Langkilde, T., Wall, M., and Mason, R. T. (2005c). The ity, and genetic correlation between the sexes. Journal of fitness correlates of scalation asymmetry in garter snakes (Tham-Heredity 92: 198–205.

nophis sirtalis parietalis). Functional Ecology 19: 306–314.

Sinsch, U. (1989). Behavioral thermoregulation of the Andean Shine, R., T. Madsen, R. L., Elphick, M. J., and Harlow, P. S.

toad (Bufo spinulosus) at high altitudes. Oecologia 80: (1997b). The influence of nest temperatures and maternal 32–38.

brooding on hatchling phenotypes of water pythons. Ecology Sites, J. W., Jr, and Crandall, K. A. (1997). Testing species 78: 1713–1721.

boundaries in biodiversity studies. Conservation Biology Shoemaker, V. H. (1992). Exchange of water, ions, and respira-11: 1289–1297.

tory gases in terrestrial amphibians. In Environmental Physi-Sites, J. W., Jr, Davis, S. K., Guerra, T., Iverson, J. B., and Snell, ology of the Amphibians. M. E. Feder and W. W. Burggren H. L. (1996). Character congruence and phylogenetic signal (Eds.). Pp. 125–150. University of Chicago Press, Chicago.

in molecular and morphological data sets: A case study in Shoemaker, V. H., and Bickler, P. E. (1979). Kidney and bladder the living iguanas (Squamata, Iguanidae). Molecular Biology function in a uricotelic treefrog (Phyllomedusa sauvagei).

and Evolution 13: 1087–1105.

Journal of Comparative Physiology 133: 211–218.

Sites, J. W., Jr., Archie, J. W., Cole, C. J., and Flores Villela, O.

Shoemaker, V. H., and McClanahan, L. L. (1980). Nitrogen (1992). A review of phylogenetic hypotheses for lizards of excretion and water balance in amphibians of Borneo.

the genus Sceloporus (Phrynosomatidae): Implications for Copeia 1980: 446–451.

ecological and evolutionary studies. Bulletin of the American Shoemaker, V. H., and McClanahan, L. L. (1982). Enzymatic Museum of Natural History 213: 1–110.

correlates and uricotelism in tree frogs of the genus Phyllo-Slade, N. A., and Wassersug, R. J. (1975). On the evolution of medusa. Journal of Experimental Zoology 220: 163–169.

complex life cycles. Evolution 29: 568–571.

Shoemaker, V. H., and Nagy, K. A. (1977). Osmoregulation in Slowinski, J. B., and Keogh, J. S. (2000). Phylogenetic relationships amphibians and reptiles. Annual Review Physiology 39: of elapid snakes based on Cytochrome b mtDNA sequences.

449–471.

Molecular Phylogenetics and Evolution 15: 157–164.

Shoemaker, V. H., Baker, M. A., and Loveridge, J. P. (1989).

Slowinski, J. B., and Lawson, R. (2002). Snake phylogeny: Evi-Effect of water balance on thermoregulation in waterproof dence from nuclear and mitochondrial genes. Molecular Phy-frogs (Chiromantis and Phyllomedusa). Physiological Zool-logenetics and Evolution 24: 194–202.

ogy 62: 133–146.

Slowinski, J. B., Boundy, J., and Lawson, R. (2001). The phylo-Shoop, C. R. (1960). The breeding habits of the mole salaman-genetic relationships of Asian coral snakes (Elapidae: Callio-der, Ambystoma talpoideum (Holbrook), in southeastern phis and Maticora) based on morphological and molecular Louisiana. Tulane Studies in Zoology 8: 65–82.

characters. Herpetologica 57: 233–245.

Shoop, C. R. (1968). Migratory orientation of Ambystoma macu-Slowinski, J. B., Knight, A., and Rooney, A. P. (1997). Inferring spe-latum: Movements near breeding ponds and displacements of cies trees from gene trees: A phylogenetic analysis of the Elapi-migrating individuals. Biological Bulletin 135: 230–238.

dae (Serpentes) based on the amino acid sequences of venom Shubin, N. H., and Jenkins, F. A., Jr. (1995). An Early Jurassic proteins. Molecular Phylogenetics and Evolution 8: 349–362.

jumping frog. Nature 377: 49–52.

Slowinski, J. B., and Lawson, R. (2005). Elapid relationships.

Shubin, N. H., Daeschler, E. B., and Coates, M. I. (2004). The In Ecology and Evolution in the Tropics: Essays in tribute early evolution of the tetrapod humerus. Science 304: 90–93.

to J.M. Savage. M. A. Donnelly, B. I. Crother, C. Guyer, Shubin, N. H., Daeschler, E. B., and Jenkins, F. A. (2006). The M. H. Wake, and M. E. White (Eds.). Pp. 174–189. Univer-pectoral fin of Tiktaalik roseae and the origin of the tetrapod sity of Chicago Press, Chicago, IL.

limb. Nature 440: 764–771.

Smatresk, N. J. (1994). Respiratory control in the transition from Simon, C. A. (1975). The influence of food abundance on terri-water to air breathing in vertebrates. American Zoologist 34: tory size in the iguanid lizard Sceloporus jarrovi. Ecology 264–279.

56: 993–998.

Smith, C. C., and Fretwell, S. D. (1974). The optimal balance Simon, M. P. (1983). The ecology of parental care in a terrestrial between size and number of offspring. American Naturalist breeding frog from New Guinea. Behavioral Ecology and 108: 499–506.

Sociobiology 14: 61–67.

Smith, H. M., Smith, R. B., and Sawin, H. L. (1977). A summary Simon, M. P., and Toft, C. A. (1991). Diet specialization in small of snake classification (Reptilia, Serpentes). Journal of Her-vertebrates: Mite eating in frogs. Oikos 61: 263–278.

petology 11: 115–121.

Simons, R. S., and Brainerd, E. L. (1999). Morphological varia-Smith, M. A. (1943). The Fauna of British India, Ceylon and tion of hypaxial musculature in salamanders (Lissamphibia: Burma. Vol. III. Serpentes. Taylor and Francis, London.

Caudata). Journal of Morphology 241: 153–164.

Smith, R. B., Breininger, D. R., and Larson, V. L. (1997). Home Simpson, G. G. (1961). Principles of Animal Taxonomy. Colum-range characteristics of radiotagged gopher tortoises on Ken-bia University Press, New York.

nedy Space Center, Florida. Chelonian Conservation and Sinch, U. (1990). Migration and orientation in anuran amphi-Biology 2: 358–362.

bians. Ethology, Ecology & Evolution 2: 65–79.

Smith, S. A., Arif, S., de Oca, A. N. M., and Wiens, J. J. (2007).

Sinervo, B., and Zamudio, K. R. (2001). The evolution of alter-A phylogenetic hot spot for evolutionary novelty in middle native reproductive strategies: Fitness differential, heritabil-American treefrogs. Evolution 61: 2075–2085.

Smith, S. M. (1975). Innate recognition of coral snake pattern by Stamps, J. A. (1983). Sexual selection, sexual dimorphism, and a possible avian predator. Science 187: 759–760.

territoriality. In Lizard Ecology. Studies of a Model Organ-Smith, S. M. (1977). Coral-snake pattern recognition and stimu-ism. R. B. Huey, E. R. Pianka, and T. W. Schoener (Eds.).

lus generalisation by naive great kiskadees (Aves: Tyranni-Pp. 169–204. Harvard University Press, Cambridge, Mass.

dae). Nature 265: 535–536.

Stamps, J. A., Krishnan, V. V., and Andrews, R. M. (1994). Ana-Smith, T. L., Povel, G. D. E., and Kardong, K. V. (2002). Preda-lyses of sexual size dimorphism using null growth-based tory strike of the tentacled snake (Erpeton tentaculatum).

models. Copeia 1994: 598–613.

Journal of Zoology, London 256: 233–242.

Stamps, J. A., Mangel, M., and Phillips, J. A. (1998). A new look Snell, H. L., and Tracy, C. R. (1985). Behavioral and morpholog-at relationships between size at maturity and asymptotic size.

ical adaptations by Galapagos land iguanas (Conolophus sub-American Naturalist 152: 470–479.

cristatus) to water and energy requirements of eggs and Stamps, J., and Krishnan, V. V. (1997). Sexual bimaturation and neonates. American Zoologist 25: 1009–1018.

sexual size dimorphism in animals with asymptotic growth Sokal, R. R. (1986). Phenetic taxonomy: Theory and methods.

after maturity. Evolutionary Ecology 11: 21–39.

Annual Review of Evology and Systematics 17: 423–442.

Starace, F. (1998). Guide des Serpents et Amphisbènes de Som, C., and Reyer, H. U. (2007). Hemiclonal reproduction Guyana Franc¸aise. Ibis Rouge Editions, Guadeloupe.

slows down the speed of Muller’s ratchet in the hybridoge-Stearns, S. C. (1976). Life-history tactics: A review of the ideas.

netic frog Rana esculenta. Journal of Evolutionary Biology Quarterly Review of Biology 51: 3–47.

20: 650–660.

Stearns, S. C. (1977). The evolution of life history traits: A cri-Somma, L. A. (2003). Parental Behavior in Lepidosaurian and tique of the theory and a review of the data. Annual Review Testudinian Reptiles. Krieger Publishing Company, Malabar, of Ecology and Systematics 8: 145–171.

Florida.

Stearns, S. C. (1992). The Evolution of Life Histories. Oxford Somma, L. A., and Fawcett, J. D. (1989). Brooding behaviour of University Press, Oxford.

the prairie skink, Eumeces septentrionalis, and its relation-Stebbins, R. C.

(1954). Amphibians and Reptiles of Western ship to the hydric environment of the nest. Zoological Jour-North America. McGraw-Hill Book Co., Inc, New York.

nal of the Linnean Society 95: 245–256.

Stebbins, R. C., and Cohen, N. W. (1995). A Natural History of Spellerberg, I. F. (1988). Ecology and management of Lacerta Amphibians. Princeton University Press, Princeton.

agilis L. populations in England. Mertensiella 1: 113–121.

Steel, R. (1973). Crocodylia. Handbuch der Palaöherpetologie, Spinar, Z. V. (1972). Tertiary Frogs from Central Europe.

16. Gustav Fischer Verlag, Stuttgart.

W. Junk N. V, The Hague.

Stein, K., Palmer, C., Gill, P., and Benton, M. (in press). The Spotila, J. R., Dunham, A. E., Leslie, A. J., Steyermark, A. C., aerodynamics of the Late Triassic British Kuehneosauridae.

Plotkin, P. T., and Paladino, F. V. (1998). Worldwide popu-Paleontology in press.

lation decline of Dermochelys coriacea: Are leatherback sea-Stephens, P. R., and Wiens, J. J. (2003). Ecological diversifica-turtles going extinct? Chelonian Conservation Biology 2: tion and phylogeny of emydid turtles. Biological Journal of 209–222.

the Linnean Society 79: 577–610.

Spotila, J. R., O'Connor, M. P., and Bakken, G. S. (1992).

Stephens, P. R., and Wiens, J. J. (2004). Convergence, diver-Biophysics of heat and mass transfer. In Environmental gence, and homogenization in the ecological structure of Physiology of the Amphibians. M. E. Feder and W. W.

emydid turtle communities: The effects of phylogeny and Burggren (Eds.). Pp. 59–80. University of Chicago Press, dispersal. American Naturalist 164: 244–254.

Chicago.

Steubing, R. (1994). A new species of Cylindrophis (Serpentes: Spotila, J.

R., O'Connor, M. P., and Paladino, F. V. (1997). Ther-Cylindrophiidae) from Sarawak, western Borneo. Raffles mal biology. In The Biology of Sea Turtles. P. L. Lutz and Bulletin of Zoology 42: 967–973.

J. A. Musick (Eds.). Pp. 297–314. CRC Press, Boca Raton, FL.

Stewart, J. R. (1989). Facultative placentotrophy and the evolu-Spotila, J. R., Terpin, K. M., and Dodson, P. (1977). Mouth tion of squamate placentation: Quality of eggs and neonates gaping as an effective thermoregulatory device in alligators.

in Virginia striatula. American Naturalist 133: 111–137.

Nature 265: 235–236.

Stewart, J. R., and Blackburn, D. G. (1988). Reptilian placentation: Sprawl, S., and Branch, B. (1995). The Dangerous Snakes of structural diversity and terminology. Copeia 1988: 839–852.

Africa. Ralph Curtis Books, Sanibel Island, FL.

Stewart, J. R., and Thompson, M. B. (1996). Evolution of reptil-Spray, D. C. (1976). Pain and temperature receptors of anurans.

ian placentation: development of extraembryonic membranes In Frog Neurobiology. A Handbook. R. Llinaś and W. Precht of the Australian scincid lizards, Bassiana duperreyi (ovipa-

(Eds.). Pp. 607–628. Springer-Verlag, Berlin.

rous) and Pseudemoia entrecasteauxii (viviparous). Journal Stammer, D. (1976). Reptiles. In Around Mt. Isa. A Guide to the of Morphology 227: 349–370.

Flora and Fauna. H. Horton (ed.) University of Queensland, Stewart, J. R., and Thompson, M. B. (2000). Evolution of placen-St Lucia, Queensland.

tation among squamate reptiles: Recent research and future Stamps, J. A. (1977). Social behavior and spacing patterns in directions. Comparative Biochemistry and Physiology Part lizards. In Biology of the Reptilia. Volume 7. Ecology and A 127: 411–431.

Behavior. C. Gans and D. W. Tinkle (Eds.). Pp. 265–334.

Stewart, J. R., and Thompson, M. B. (2003). Evolutionary trans-Academic Press. New York.

formations of the fetal membranes of viviparous reptiles: Stamps, J. A. (1978). A field study on the ontogeny of social A case study of two lineages. Journal of Experimental Zool-behavior in the lizard Anolis aeneus. Behaviour 64: 1–31.

ogy 299A: 13–32.

Stewart, M. M. (1967). Amphibians of Malawi. State University Sullivan, R. M., and Estes, R. (1997). A reassessment of the fos-of New York Press, New York.

sil Tupinambinae. In Vertebrate Paleontology in the Neo-Stewart, M. M. (1974). Parallel pattern polymorphism in the genus tropics. The Miocene Fauna of La Venta, Colombia. R. F.

Phrynobatrachus (Amphibia: Ranidae). Copeia 1974: 823–832.

Kay, R. H. Madden, R. L. Cifelli, and J. J. Flynn (Eds.).

Stewart, M. M., and Pough, F. H. (1983). Population density of trop-Pp. 100–112. Smithsonian Institute Press, Washington, DC.

ical forest frogs: Relation to retreat sites. Science 221: 570–571.

Sullivan, R. M., and Holman, J. A. (1996). Squamata. In The Steyn, W. (1963). Angolocaurus [sic] skoogi (Andersson)—a Terrestrial Eocene-Oligocene Transition in North America.

new record from south west Africa. Cimbebasia 6: 8–11.

D. R. Prothero and R. J. Emry (Eds.). Pp. 354–372. Cam-Stickel, L. F. (1950). Populations and home range relationships bridge University Press, New York.

of the box turtle Terrapene c. carolina (Linnaeus). Ecologi-Sumida, S. S. (1997). Locomotor features of taxa spanning the cal Monographs 20: 351–378.

origin of amniotes. In Amniote Origins. Completing the Tran-Stickel, L. F. (1989). Home range behavior among box turtles sition to Land. S. S. Sumida and K. L. M. Martin (Eds.)

K. L. M. Martin (Eds.).

(Terrapene c. carolina) of a bottomland forest in Maryland.

Pp. 353–398. Academic Press, San Diego.

Journal of Herpetology 23: 40–44.

Sumida, S. S., and Martin, K. L. M. (2000). Amniote Origins. Com-Stocks, A., McMahan, B., and Taber, P. (2007). Indigenous, col-pleting the Transition to Land. Academic Press, San Diego, CA.

onist, and government impacts on Nicaragua’s Bosawas Summers, A. P., and O’Reilly, J. C. (1997). A comparative study reserve. Conservation Biology 21: 1495–1505.

of locomotion in the caecilians Dermophis mexicanus and Stockwell, D., and Peters, D. (1999). The GARP modelling sys-Typhlonectes natans (Amphibia: Gymnophiona). Zoological tem: Problems and solutions to automated spatial prediction.

Journal of the Linnean Society 121: 65–76.

International Journal of Geographical Information Science Summers, K. (2003). Convergent evolution of bright coloration 13: 143–158.

and toxicity in frogs. Proceedings of the National Academy Stone, P. A. (2001). Movements and demography of the Sonoran of Sciences (USA) 100: 12533–12534.

mud turtle, Kinosternon sonoriense. Southwestern Naturalist Summers, K., and Amos, W. (1997). Behavioral, ecological, and 46: 41–53.

molecular genetic analyses of reproductive strategies in the Storrs, G. W. (1993). Function and phylogeny in sauropterygian Amazonian dart-poison frog, Dendrobates ventrimaculatus.

(Diapsida) evolution. American Journal of Science 293–A: Behavioral Ecology 8: 260–267.

63–90.

Summers, K., and Clough, M. E. (2001). The evolution of color-Stru¨ssmann, C., Ribeiro, R. A. K., Ferreira, V. L., and Be´da, A. de F.

ation and toxicity in the poison frog family (Dendrobatidae).

(2007). Herpetofauna do Pantanal brasiliero. In Herpetologia no Proceedings

(2007). Herpetofauna do Pantanal brasileiro. In Herpetologia no Proceedings of the National Academy of Sciences (USA) 98: Brasil II. L. B. Nascimento and M. E. Oliveira (Eds.). Pp. 66–84.

6227–6232.

Sociedade Brasileira de Herpetologica, Belo Horizonte.

Summers, K., and Earn, D. J. D. (1999). The cost of polygyny Stuart, B. L., and Parham, J. F. (2004). Molecular phylogeny of the and the evolution of female care in poison frogs. Biological critically endangered Indochinese box turtle (Cuora galbini-Journal of the Linnean Society 66: 515–538.

frons). Molecular Phylogenetics and Evolution 31: 164–177.

Summers, K., and McKeon, C. S. (2004). The evolutionary ecol-Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodri-ogy of phytotelmata use in Neotropical poison frogs. Miscel-gues, A. S. L., Fischman, D. L., and Waller, R. W. (2004).

laneous Publications Museum of Zoology University of Status and trends of amphibian declines and extinctions Michigan 193: 55–73.

worldwide. Science 306: 1783–1786.

Swan, G. (1990). A Field Guide to the Snakes and Lizards of Stuebing, R. B., and Inger, R. F. (1999). A Field Guide to the New South Wales. Three Sisters Productions, Sydney, New Snakes of Borneo. Natural History Publications (Borneo), South Wales, Australia.

Kota Kinabalu.

Swart, C. C., and de Sa, R. O. (1999). The chondrocranium of the Sues, H.-D., Clark, J. M., and Jenkins, F. A., Jr. (1994). A review of Mexican burrowing toad, Rhinophrynus dorsalis. Journal of the Early Jurassic tetrapods from the Glen Canyon Group of Herpetology 33: 23–28.

the American Southwest. In In the shadow of the dinosaurs.

Swingland, I. R. (1977). Reproductive effort and life history Early Mesozoic Tetrapods. N. C. Fraser and H.-D. Sues strategy of the Aldabran giant tortoise. Nature 269: 402–404.

(Eds.). Pp. 284–294. Cambridge University Press, New York.

Swingland, I. R., and Klemens, M. W. (Eds.). (1989). The con-Sues, H.-D., Clark, J. M., and Jenkins, F. A. (1994). A review of servation biology of tortoises. Occasional Papers of the the Early Jurassic tetrapods from the Glen Canyon Group of Internation Union for Conservation of Nature Species the American Southwest. In In the Shadow of the Dinosaurs: Survival Commission 1: 1–202.

Early Mesozoic Tetrapods. N. C. Fraser and H.-D. Sues Swofford, D. L., Olsen, G. J., Waddell, P. J., and Hillis, D. M.

(Eds.). Pp. 284–294. Cambridge University Press, New York.

(1996). Phylogenetic inference. In Molecular Systematics, Sec-Sullivan, B. K. (1989). Desert environments and the structure of ond Edition. D. M. Hillis, C. Moritz, and B. K. Mable (Eds.).

anuran mating systems. Journal of Arid Environments 17: Pp. 321–381. Sinauer Associates, Inc., Sunderland, Mass.

175–183.

Sylber, C. K. (1988). Feeding habits of the lizard Sauromalus Sullivan, B. K., Ryan, M. J., and Verrell, P. A. (1995). Female varius and S. hispidus in the Gulf of California. Journal of choice and mating system structure. In Amphibian Biology.

Herpetology 22: 413–424.

Volume 2, Social Behaviour. H. Heatwole and B. K. Sullivan Taigen, T. L., Pough, F. H., and Stewart, M. M. (1984). Water (Eds.). Pp. 468–517. Surrey Beatty & Sons Pty Ltd., Chip-balance of terrestrial anuran (Eleutherodactylus coqui) eggs: ping Norton Pty Ltd, N.S.W.

Importance of parental care. Ecology 65: 248–255.

Taigen, T. L., Wells, K. D., and Marsh, R. L. (1985). The enzy-Physiology B-Biochemical Systemic and Environmental matic basis of high metabolic rates in calling frogs. Physio-Physiology 176: 179–189.

logical Zoology 58: 719–726.

Thomson, K. S. (1980). The ecology of Devonian lobe-finned Tanaka, K. (1989). Mating strategy of male Hynobius nebulosus.

fishes. In The Terrestrial Environment and the Origin of In Current Herpetology in East Asia. M. Matsui *et al.* (Eds.).

Land Vertebrates. A. L. Panchen (Ed.). Pp. 87–122. Aca-Pp. 437–448. Herpetological Society of Japan, Koyoto.

demic Press, London.

Taplin, L. E., Grigg, G. C., Harlow, P., Ellis, T. M., and Dunson, Thomson, K. S. (1993). The origin of the tetrapods. American W. A. (1982). Lingual salt glands in Crocodylus acutus and Journal of Science 293–A: 33–62.

Crocodylus johnstoni and their absence from Alligator mis-Thorbjarnarson, J. (1992). Crocodiles: An Action Plan for Their sissipiensis and Caiman crocodilus. Journal of Comparative Conservation. IUCN, Gland.

Physiology 149: 43–47.

Thorbjarnarson, J. (1996). Reproductive characteristics of the Tarsitano, S. F., Frey, E., and Riess, J. (1989). The evolution of order Crocodylia. Herpetologica 52: 8–24.

the Crocodilia: A conflict between morphological and bio-Thorbjarnarson, J. (1999). Crocodile tears and skins: Interna-chemical data. American Zoologist 29: 843–856.

tional trade, economic constraints, and limits to the sustain-Tarsitano, S., and Hecht, M. K. (1980). A reconsideration of the able

use

of

crocodilians.

Conservation

Biology

13:

reptilian relationships of Archeopteryx. Zoological Journal of 465–470.

the Linnean Society 69: 149–182.

Thorbjarnarson, J. B. (1990). Notes on the feeding behavior of Tarsitano, S., and Riess, J. (1982). Plesiosaur locomotion — the gharial (Gavialis gangeticus) under semi-natural condi-underwater flight versus rowing. Nues Jahrbuch fu¨r Geologie tions. Journal of Herpetology 24: 99–100.

und Palaöntologie, Abhandlungen 164: 188–192.

Thorpe, R. S. (1976). Biometric analysis of geographic variation Tattersall, G. J., and Gerlach, R. M. (2005). Hypoxia progres-and racial affinities. Biological Review 51: 407–452.

sively lowers thermal gaping thresholds in bearded dragons, Thorpe, R. S. (1987). Geographic variation: A synthesis of cause, Pogona vitticeps. Journal of Experimental Biology 208: data, pattern and congruence in analysis and phylogenesis.

3321–3330.

Bollettino di Zoologia 54: 3–11.

Tattersall, G. J., Cadena, V., and Skinner, M. C. (2006). Respira-Thorpe, R. S., Wu¨ster, W., and Malhotra, A. (Eds.) (1997). Ven-tory cooling and thermoregulatory coupling in reptiles.

omous Snakes. Ecology, Evolution and Snakebite. Zoological Respiratory Physiology & Neurobiology 154: 302–318.

Society of London, London.

Taylor, D. H., and Adler, K. (1973). Spatial orientation by sala-Tiebout, H. M., and Cary, J. R. (1987). Dynamic spatial ecology manders using plane polarized light. Science 181: 285–287.

of the water snake, Nerodia sipedon. Copeia 1987: 1–18.

Taylor, E. H. (1968). The Caecilians of the World. A Taxonomic Tiedemann, F. (1990). Lurche und Kriechtiere Wiens. J & V Edi-Review. University of Kansas Press, Lawrence, KS.

tions, Wien.

Tchernov, E. (1986). E´volution des Crocodiles en Afrique du Tihen, J. A. (1965). Evolutionary trends in frogs. American Zool-Nord et de l’Est. E

´ dit. Centre National de la Recherche ogist 5: 309–318.

dit. Centre National de la Recherche ogist 3: 309–318.

Scientifique, Paris.

Tilley, S. G. (1980). Life histories and comparative demography Teather, K. L. (1991). The relative importance of visual and of two salamander populations. Copeia 1980: 806–812.

chemical cues for foraging on newborn blue-striped garter Tilley, S. G., and Bernardo, J. (1993). Life history evolution in snakes

(Thamnophis

sirtalis

similis).

Behaviour

117:

plethodontid salamanders. Herpetologica 49: 154–163.

255–261.

Tilley, S. G., Lundrigan, B. L., and Brower, L. P. (1982). Ery-Temple, S. A. (1991). Conservation biology: New goals and new thrism and mimicry in the salamander Plethodon cinereus.

patterns for managers of biological resources. In “Challenges Herpetologica 38: 409–417.

in the Conservation of Biological Resources: A Practioner’s Tinkle, D. W. (1967). The life and demography of the side-Guide” D. J. Decker, M. E. Krasney, G. R. Goff, C. R.

blotched lizard, Uta stansburiana. Miscellaneous Publica-Smith, and D. W. Goss (Eds.), Pp. 45–54. Westview Press, tions of the Museum of Zoology, University of Michigan Boulder, Co.

132: 1–182.

Templeton, A. L. (1986). Coadaptation and outbreeding depres-Tinkle, D. W., and Gibbons, J. W. (1977). The distribution and sion. In Conservation Biology: The Science of Scarcity and evolution of viviparity in reptiles. Miscellaneous Publications Diversity. M. E. Soule´ (Ed.). Pp. 105–116. Sinauer

Associ-of the Museum of Zoology, University of Michigan 154: 1–55.

ates, Sunderland, MA.

Tinkle, D. W., and Hadley, N. F. (1973). Reproductive effort and Thomas, M., Raharivololoniaina, L., Glaw, F., Vences, M., and winter activity in the viviparous montane lizard Sceloporus Vieites, D. R. (2005). Montane tadpoles in Madagascar: jarrovi. Copeia 1973: 272–277.

Molecular identification and description of the larval stages Tinkle, D. W., and Hadley, N. F. (1975). Lizard reproductive of Mantidactylus elegans, Mantidactylus madecassus, and effort: caloric estimates and comments on its evolution. Ecol-Boophis laurenti from the Andringitra Massif. Copeia ogy 56: 427–434.

2005: 174–183.

Tinkle, D. W., Congdon, J. D., and Rosen, P. C. (1981). Nesting Thomas, R. (1965). A congregation of the blind snake, Typhlops frequency and success: Implications for the demography of richardi. Herpetologica 21: 309.

painted turtles. Ecology 62: 1426–1432.

Thompson, M. B., and Speake, B. K. (2006). A review of the Tinkle, D. W., Wilbur, H. M., and Tilley, S. G. (1970). Evolu-evolution of viviparity in lizards: Structure, function and tionary strategies in lizard reproduction. Evolution 24: physiology

of

the

placenta.

Journal

of

Comparative

55–74.

Tinsley, R. C. (1990). The influence of parasite infection on mat-Tong, H., Gaffney, E. S., and Buffetaut, E. (1998). Foxemys, a ing success in spadefoot toads, Scaphiopus couchii. Ameri-new side-neck turtle (Bothremydidae: Pelomedusoides) from can Zoologist 30: 313–324.

the Late Cretaceous of France. American Museum Novitates Tinsley, R. C. and Kobel, H. R. (Eds.) (1996). The Biology of 3251: 1–19.

Xenopus. Zoological Society of London, London.

Toranzo, G. S., Oterino, J., Zelarayan, L., Bonilla, F., and Buh-Tinsley, R. C., Loumont, C., and Kobel, H. R. (1996). Geoler, M. I. (2007). Spontaneous and LH-induced maturation graphic distribution and ecology. In The Biology of Xenopus.

in Bufo arenarum oocytes: Importance of gap junctions.

R. C. Tinsley and H. R. Kobel (Eds.). Pp. 34–59. Zool. Soc.

Zygote 15: 65–80.

London, London.

Torres-Carvajal, O. (2007). Phylogeny and biogeography of a Titus, T. A., and Frost, D. R. (1996). Molecular homology assess-large radiation of Andean lizards (Iguania, Stenocercus).

ment and phylogeny in the lizard family Opluridae (Squamata: Zoologica Scripta 36: 311–326.

Iguania). Molecular Phylogenetics and Evolution 6: 49–62.

Torres-Carvajal, O., Schulte, J. A., and Cadle, J. E. (2006). Phy-Titus, T. A., and Larson, A. (1995). A molecular phylogenetics logenetic relationships of South American lizards of the perspective on the evolutionary radiation of the salamander genus Stenocercus (Squamata: Iguania): A new approach family Salamandridae. Systematic Biology 44: 125–151.

using a general mixture model for gene sequence data.

Titus, T. A., and Larson, A. (1997). Molecular phylogenetics of Molecular Phylogenetics and Evolution 39: 171–185.

desmognathine salamanders (Caudata: Plethodontidae): A Touchon, J. C., Gomez-Mestre, I., and Warkentin, K. M. (2006).

reevaluation of evolution in ecology, life history, and mor-Hatching plasticity in two temperate anurans: Responses to a phology. Systematic Biology [1996] 45: 451–472.

pathogen and predation cues. Canadian Journal of Zoology Tobias, M. L., Viswanathan, S. S., and Kelley, D. B. (1998).

84: 556–563.

Rapping, a female receptive call, initiates male-female duets Townsend, D. S., and Stewart, M. M. (1985). Direct development in the South African clawed frog. Proceedings of the in Eleutherodactylus coqui (Anura: Leptodactylidae): A National Academy of Sciences (USA) 95: 1870–1875.

staging table. Copeia 1985: 423–436.

Toft, C. A. (1980). Feeding ecology of thirteen syntopic species Townsend, D. S., Stewart, M. M., Pough, F. H., and Brussard, of anurans in a seasonal tropical environment. Oecologia 45: P. F. (1981). Internal fertilization in an oviparous frog. Sci-131–134.

ence 212: 469–471.

Toft, C. A. (1995). Evolution of diet specialization in poison-dart Townsend, T. M., Larson, A., Louis, E., and Macey, J. R. (2004).

frogs (Dendrobatidae). Herpetologica 51: 202–216.

Molecular phylogenetics of Squamata: The position of Tokar, A. A. (1989). A revision of the genus Eryx (Serpentes, snakes, Amphisbaenians, and Dibamids, and the root of the Boidae), based upon osteological data. Vestnik Zoologii Squamate tree. Systematic Biology 53: 735–757.

1989: 46–55.

Tracy, C. R. (1971). Evidence for the use of celestial cues by dis-Tokar, A. A. (1996). Taxonomic revision of the genus Gongylo-persing immature California toads (Bufo boreas). Copeia phis Wagler 1830: G. colubrinus (L. 1758) (Serpentes Boi-1971: 145–147.

dae). Tropical Zoology 9: 1–17.

Tracy, C. R., and Christian, K. A. (2005). Preferred temperature Tokarz, R. R. (1992). Male mating preferences for unfamiliar correlates with evaporative water loss in hylid frogs from females in the lizard Anolis sagrei. Animal

Behaviour 44: northern Australia. Physiological and Biochemical Zoology 843–849.

78: 839–846.

Tokarz, R. R. (1995). Mate choice in lizards: A review. Herpeto-Tracy, C. R., and Dole, J. W. (1969). Orientation of displaced logical Monographs 9: 17–40.

California toads, Bufo boreas, to their breeding sites. Copeia Toledo, L. F. (2005). Predation of juvenile and adult anurans by 1969: 693–700.

invertebrates: Current knowledge and perspectives. Herpeto-Tracy, C. R., Nussear, K. E., Esque, T. C., Dean-Bradley, K., logical Review 36: 395–400.

DeFalco, L. A., Castle, K. T., Zimmerman, L. C., Espinoza, Toledo, L. F., Ribeiro, R. S., and Haddad, C. F. B. (2007). Anur-R. E., and Barber, A. M. (2006). The importance of physio-ans as prey: An exploratory analysis and size relationships logical ecology in conservation biology. Integrative and between predators and their prey. Journal of Zoology, Lon-Comparative Biology 46: 1191–1205.

don 271: 170–177.

Trauth, S. E., Cooper, J., Vitt, L. J., and Perrill, S. A. (1987).

Tolley, K., A., Tilbury, C. R., Branch, W. R., and Matthee, C. A.

Cloacal anatomy of the broad-headed skink, Eumeces lati-

(2004). Phylogenetics of the southern African dwarf chame-ceps, with a description of a female pheromonal gland. Her-leons, Bradypodion (Squamata: Chamaeleonidae). Molecular petologica 43: 458–466.

Phylogenetics and Evolution 30: 354–365.

Trivers, R. L. (1972). Parental investment and sexual selection.

Tolson, P. J., and Henderson, R. W. (1993). The Natural History In Sexual Selection and the Descent of Man. B. Campbell of West Indian Boas. R&A Publishing, Ltd, Taunton, U.K.

(Ed.). Pp. 136–179. Aldine, Chicago.

Tome, M. A., and Pough, F. H. (1982). Responses of amphibians Trivers, R. L. (1976). Sexual selection and resource-accruing to acid precipitation. In Acid Rain/Fisheries. Proceedings of abilities in Anolis garmani. Evolution 30: 253–

Kam/Fisheries. Proceedings of abilities in Anolis garmani. Evolution 36: 253–269.

an International Symposium on Acidic Precipitation and Trontelj, P., and Goricki, S. (2003). Monphyly of the family Protei-Fishery Impacts in Northeastern North America. R. E. John-dae (Amphibia: Caudata) tested by phylogenetic analysis of son (Ed.). Pp. 245–254. American Fisheries Society, mitochondrial 12s rDNA sequences. Natura Croatica 12: Bethesda, Md.

113–120.

Troyer, K. (1984a). Structure and function of the digestive tract Tyler, M. J. (1991a). Kyarranus Moore (Anura, Leptodactylidae) of an herbivorous lizard Iguana iguana. Physiological Zool-from the Tertiary of Queensland. Proceedings of the Royal ogy 57: 1–8.

Society of Victoria 103: 47–51.

Troyer, K. (1984b). Behavioral acquisition of the hindgut fer-Tyler, M. J. (1991b). Hylid frogs from the mid-Miocene mentation system by hatchling Iguana iguana. Behavioral Camfield Beds of northern Australia. The Beagle 11: Ecology and Sociobiology 14: 189–193.

141–144.

Trueb, L. (1973). Bones, frogs, and evolution. In Evolutionary Tyler, M. J. (1991c). Declining amphibian populations – a global Biology of the Anurans. J. L. Vial (Ed.). Pp. 65–132. Univer-phenomenon? An Australian perspective. Alytes 9: 43–50.

sity of Missouri Press, Columbia.

Tyler, M. J., and Davies, M. (1978). Phylogenetic relationships Trueb, L. (1974). Systematic relationships of Neotropical horned of Australian hyline and neotropical phyllomedusine frogs frogs, genus Hemiphractus (Anura: Hylidae). Occasional of the family Hylidae. Herpetologica 34: 219–224.

Papers of the Museum of Natural History, University of Kan-Tyler, M. J., and Davies, M. (1993). The Hylidae. In Fauna of sas 29: 1–60.

Australia. Volume 2A. Amphibia & Reptilia. C. J. Gasby, Trueb, L., and Cannatella, D. C. (1986). Systematics, morphol-G. J. B. Ross, and P. L. Beesley (Eds.). Pp. 58–63. Australian ogy, and phylogeny of genus Pipa (Anura: Pipidae). Herpe-Government Publishing Service, Canberra.

tologica 42: 412–449.

Tyler, M. J., and Duellman, W. E. (1995). Superficial mandibular Trueb, L., and Cloutier, R. (1991a). Toward an understanding of musculature and vocal sac structure in hemiphractine hylid the amphibians: Two centuries of systematic history.

frogs. Journal of Morphology 224: 65–71.

In Origins of the Higher Groups of Tetrapods. Controversy Tyrrell, C. (2001). Completion of research on reproductive ecol-and Consensus. H.-P. Schultze and L. Trueb (Eds.).

ogy of tuatara on northern islands, including Aorangi, Tar-Pp. 176–193. Comstock Publishing Associates, Ithaca, NY.

anga and the Marotere Islands. 141. University of Otago, Trueb, L, and Cloutier, R. (1991b). A phylogenetic investigation Dunedin.

of the inter-and intrarelationships of the Lissamphibia Udvardy, M. D. F. (1975). A classification of the Biogeographi-

(Amphibia: Temnospondylii). In Origins of the Higher cal Provinces of the World. IUCN Occasional Paper no. 18.

Groups of Tetrapods. Controversy and Consensus. H.-P.

Morges, Switzerland.

Schultze and L. Trueb (Eds.). Pp. 223–313. Comstock Pub-Uetz, P. (1999). The EMBL reptile database. www.embl-heildberg.

lishing Associates, Ithaca, NY.

de/~uetz/LivingReptiles.html.

Trueb, L., and Gans, C. (1983). Feeding specializations of the Ugarte, C. A., Rice, K. G., and Donnelly, M. A. (2007). Compar-Mexican burrowing toad, Rhinophrynus dorsalis (Anura: ison of diet, reproductive biology, and growth of the pig frog Rhinophrynidae). Journal of Zoology, London 199: 189–208.

(Rana grylio) from harvested and protected areas of the Flor Tsuji, H., and

(Rana grylio) from harvested and protected areas of the Hori-Tsuji, H., and Lue, K. Y. (1998). Temporal aspects of the ida everglades. Copeia 2007: 436–448.

amplexus and oviposition behavior of the fanged frog Rana Ultsch, G. R., Bradford, D. F., and Freda, J. (1999). Physiology: kuhlii from Taiwan. Copeia 1998: 769–773.

Coping with the environment. In Tadpoles: The Biology of Tu, M.-C., Chu, C.-W., and Lue, K.-Y. (1999). Specific gravity Anuran Larvae. R. W. McDiarmid and R. Altig (Eds.).

and mechanisms for its control in tadpoles of three anuran Pp. 189–214. University of of Chicago Press, Chicago.

species from different water strata. Zoological Studies 38: Underwood, G. (1967). A Contribution to the Classification of 76–81.

Snakes. British Museum of Natural History, London.

Tuberville, T. D., Gibbons, J. W., and Greene, J. L. (1996). Inva-Underwood, G. (1970). The eye. In Biology of the Reptilia. Vol-sion of new aquatic habitats by male freshwater turtles.

ume 2. Morphology B. C. Gans and T. S. Parsons (Eds.).

Copeia 1996: 713–715.

Pp. 1–97. Academic Press, London.

Turner, F. B. (1977). The dynamics of populations of squamates, Underwood, G., and Kochva, E. (1993). On the affinities of the crocodilians and rhynchocephalians. In Biology of the Repti-burrowing asps Atractaspis (Serpentes: Atractaspididae).

lia. Volume 7. Ecology and Behavior. C. Gans and D. W.

Zoological Journal of the Linnean Society 107: 3–64.

Tinkle (Eds.). Pp. 157–264. Academic Press, New York.

Underwood, G., and Stimson, A. F. (1990). A classification of Turner, F. B., Medica, P. A., Lannom, J. R., Jr., and Hodden-pythons (Serpentes, Pythoninae). Journal of Zoology, London bach, G. A. (1969). A demographic analysis of fenced popu-221: 565–603.

lations of the whiptailed lizard, Cnemidophorus tigris, in Urban, M., Phillips,

B. L., Skelly, D. K., and Shine, R. (2007).

southern Nevada. Southwestern Naturalist 14: 189–202.

The cane toad's (Chaunus marinus) increasing ability to Tuttle, M. D., and Ryan, M. J. (1981). Bat predation and the evo-invade Australia is revealed by a dynamically updated range lution of frog vocalization in the Neotropics. Science 214: model. Proceedings of the Royal Society London Series B

677–678.

274: 1413–1419.

Twitty, V. C. (1966). Of Scientists and Salamanders. W. H. Free-Valenzuela, N. (2004). Evolution and maintenance of tempera-man & Co, San Francisco.

ture-dependent sex determination. In Temperature-Depen-Tyler, M. J. (1985). Reproductive modes in Australian Amphibia.

dent Sex Determination in Vertebrates. N. Valenzuela and In Biology of Australasian Frogs and Reptiles. G. Grigg, R.

V. Lance (Eds.). Pp. 131–147. Smithsonian Books, Washing-Shine, and H. Ehmann (Eds.). Pp. 265–267. Surrey Beatty & ton, D. C.

Sons Pty Ltd, Chipping Norton Pty Ltd., Sydney, Australia.

Valenzuela, N. and Lance, V. (Eds.) (2004). Temperature-depen-Tyler, M. J. (1989). Australian Frogs. Viking O'Neil, Ringwood, dent Sex Determination in Vertebates. Smithsonian Books, Australia.

Washington D. C.

Valladares-Padua, C. (2006). Importance of knowledge-intensive of S. Paulo, Brasil. I. Introduction to the area and problems.

economic development to conservation of biodiversity in Papeís Avulsos Zoologia (Sa˜o Paulo) 26: 281–294.

developing countries. Conservation Biology 20: 700–701.

Vanzolini, P. E. (2002). A second note on the geographical dif-Van Berkum,

F. H., Huey, R. B., and Adams, B. A. (1986). Phys-ferentiation of Amphisbaena fuliginosa L., 1758 (Squamata, iological consequences of thermoregulation in a tropical liz-Amphisbaenidae), with a consideration of the forest refuge ard (Ameiva festiva). Physiological Zoology 59: 464–472.

model of speciation. Anais da Academia Brasileira de Cieˆn-van Beurden, E. K. (1984). Survival strategies of the Australian cias 74: 609–648.

water-holding frog, Cyclorana platycephalus. In Arid Austra-Vanzolini, P. E., and Williams, E. E. (1970a). South American lia. H. G. Cogger and E. E. Cameron (Eds.). Pp. 223–234.

anoles: The geographic differentiation and evolution of the Australian Museum, Sydney.

Anolis chrysolepis species group (Sauria, Iguanidae). Part 1.

Van Bocxlaer, I., Roelants, K., Biju, S. D., Nagaraju, J., and Bos-Arquivos de Zoologia 19: 1–124.

suyt, F. (2006). Late Cretaceous vicariance in Gondwanan Vanzolini, P. E., and Williams, E. E. (1970b). South American amphibians. PLos ONE 1: e74.

anoles: The geographic differentiation and evolution of the Van Damme, R., Bauwens, D., Brana, F., and Verheyen, R. F.

Anolis chrysolepis species group (Sauria, Iguanidae). Part 2.

(1992). Incubation temperature differentially affects hatching Arquivos de Zoologia 19: 125–298.

time, egg survival, and hatchling performance in the lizard Vanzolini, P. E., and Williams, E. E. (1981). The vanishing ref-Podarcis muralis. Herpetologica 48: 220–228.

uge: a mechanism for ecogeographic speciation. Papeís Avul-van den Elzen, P. (1975). Contribution a´ la connaissance de sos Zoologia (Sa˜o Paulo) 34: 251–255.

Pelodytes punctatus e´tudieén Camarque. Bulletin de la Soci-Vanzolini, P. E., Ramos-Costa, A. M. M., and Vitt, L. J. (1980).

e´te´ de Zoologique de France 100: 691–692.

Repteis das Caatingas. Academia Brasileira de Cieˆncias, Rio van der

Meijden, A., Boistel, R., Gerlach, J., Ohler, A., Vences, de Janeiro.

M., and Meyer, A. (2007a). Molecular phylogenetic evidence Vasudevan, K. (1996/97). Reproductive ecology of Aspideretes for paraphyly of the genus Sooglossus, with the description gangeticus (Cuvier) in north India. International Congress of a new genus of Seychellean frogs. Biological Journal of on Chelonian Conservation 1995, Pp. 21–28.

the Linnean Society 91: 347–359.

Vasudevan, K., Kumar, A., and Chellam, R. (2001). Structure van der Meijden, A., Vences, M., Hoegg, S., and Meyer, A.

and composition of rainforest floor amphibian communities (2005). A previously unrecognized radiation of ranid frogs in Kalakad-Mundanthurai Tiger Reserve. Current Science in Southern Africa revealed by nuclear and mitochondrial 80: 406–412.

DNA sequences. Molecular Phylogenetics and Evolution Vaughn, L. K., Bernheim, H. A., and Kluger, M. J. (1974). Fever 37: 674–685.

in the lizard Dipsosaurus dorsalis. Nature 252: 473–474.

van der Meijden, A., Vences, M., Hoegg, S., Boistel, R., Chan-Vaz-Ferreira, R., and Gehrau, A. (1975). Epimeletic behavior of ning, A., and Meyer, A. (2007b). Nuclear gene phylogeny the South American common frog Leptodactylus ocellatus of narrow-mouthed toads (Family: Microhylidae) and a dis-

(L.) (Amphibia, Leptodactylidae). I. Brood care and related cussion of competing hypotheses concerning their bio-feeding and aggressive activities. Physis Buenos Aires 34: geographical

origins.

Molecular

Phylogenetics

and

1–14.

Evolution 44: 1017–1030.

Vaz-Ferreira, R., Covelo de Zolessi, L., and Achaval, F. (1970).

Van Devender, R. W. (1982). Comparative demography of the Oviposicion y desarollo de ofidios y lacertilios en hormi-lizard Basiliscus basciliscus. Herpetologica 38: 189–208.

gueros de Acromyrmex. Physis 79: 431–459.

van Dyke, J. H. (1997). Family Gerrhosauridae. In Proceedings Veith, M., and Steinfartz, S. (2004). When non-monphyly results of the Fitzsimons Commemorative Symposium. (J. H. van in taxonomic cosequences – the case of Mertensiella with the Dyke Ed.), pp. 44–51. Herpotological Association of Africa, Salamandridae (Amphibia: Urodela). Salamandra, Rhein-Matieland, S. Afr.

bach 40: 67–80.

van Loben Sels, R. C., Congdon, J. D., and Austin, J. T. (1997).

Veith, M., Fromhage, L., Kosuch, J., and Vences, M. (2006).

Life history and ecology of the Sonoran mud turtle (Kinoster-Historical biogeography of Western Palaearctic pelobatid non sonoriense) in southeastern Arizona: A preliminary and pelodytid frogs: A molecular phylogenetic perspective.

report. Chelonian Conservation Biology 2: 338–344.

Contributions to Zoology 75: 109–120.

Van Mieriop, L. H. S., and Barnard, S. M. (1978). Further obser-Veith, M., Steinfartz, S., Zardoya, R., Seitz, A., and Meyer, A.

vations on thermoregulation in the brooding female Python (1998). A molecular phylogeny of ’true’ salamanders (family molurus

bivittatus

(Serpentes:

Boidae).

Copeia

1978:

Salamandridae) and the evolution of terrestriality of repro-615–621.

ductive modes. Journal of Zoological Systematics and Evolu-Vanhooydonck, B., Herrel, A., and Van Damme, R. (2007).

tionary Research 36: 7–16.

Interactions between habitat use, behavior, and trophic niche Vences, M., and Glaw, F. (2002a). Molecular phylogeography of of lacertid lizards. In Lizard Ecology: The Evolutionary Con-Boophis tephraeomystax: A test case for east-west vicariance sequences of Foraging Mode. S. M. Reilly, L. D. McBrayer, in Malagasy anurans (Amphibia, Anura, Mantellidae). Spixi-and D. B. Miles (Eds.). Pp. 427–449. Cambridge University ana 25: 79–84.

Press, Cambrdge UK.

Vences, M., and Glaw, F. (2002b). Two new treefrogs of the Boo-Vanzolini, P. E. (1973). Distribution and differentiation of ani-phis rappiodes group from eastern Madagascar (Amphibia mals along the coast and in continental inslands of the state Mantellidae). Tropical Zoology 15: 141–163.

Vences, M., and Glaw, F. (2005a). A new cryptic frog of the Verrell, P. A. (1982). The sexual behaviour of the red-spotted genus Boophis from the northwestern rainforests of Madagas-newt, Notopthalmus viridescens (Amphibia: Urodela: Sala-car. African Journal of Herpetology 54: 77–84.

mandridae). Animal Behaviour 30: 1224–1236.

Vences, M., and Glaw, F. (2005b). A new species of Mantidac-Verrell, P. A. (1983). The influence of the ambient sex ratio and tylus from the east coast of Madagascar and its molecular intermale competition on the sexual behavior of the red-phylogenetic relationships within the subgenus Guibemantis.

spotted newt, Notophthalmus viridescens (Amphibia, Uro-Herpetological Journal 15: 37–44.

dela: Salamandridae). Behavioral Ecology and Sociobiology Vences, M., Andreone, F., Glaw, F., Kosuch, J., Meyer, A., 13: 307–313.

Schaefer, H. C., and Veith, M. (2002). Exploring the poten-Verrell, P. A. (1989). The sexual strategies of natural populations tial of life-history key innovation: Brook breeding in the radi-of newts and salamanders. Herpetologica 45: 265–282.

ation of the Malagasy treefrog genus Boophis. Molecular Verrell, P. A., and Halliday, T. (1985). Reproductive dynamics Ecology 11: 1453–1463.

of a population of smooth newts, Triturus vulgaris, in south-Vences, M., Freyhof, J., Sonnenberg, R., Kosuch, J., and Veith, ern England. Herpetologia 41: 386–395.

M. (2001). Reconciling fossils and molecules: Cenozoic Vertucci, F. A., and Corn, P. S. (1996). Evaluation of episodic divergence of cichlid fishes and the biogeography of Mada-acidification and amphibian declines in the Rocky Moun-gascar. Journal of Biogeography 28: 1091–1099.

tains. Ecological Applications 6: 449–457.

Vences, M., Glaw, F., and Boehme, W. (1999). A review of the Vial, J. L. (1968). The ecology of the tropical salamander, Boli-genus Mantella (Anura, Ranidae, Mantellinae): Taxonomy, toglossa subpalmata, in Costa Rica. Revista de Biologıá distribution and conservation of Malagasy poison frogs.

Tropical 15: 13–115.

Alytes (Paris) 17: 3–72.

Vial, J. L., Berger, T. J., and McWilliams, W. T. (1977). Quanti-Vences, M., Glaw, F., and Bo¨hme, W. (1997/98). Evolutionary tative demography of copperheads, Agkistrodon contortrix.

correlates

of

microphagy

in

alkaloid-containing

frogs

Researches on Population Ecology 18: 223–234.

(Amphibia: Anura). Zoologischer Anzeiger 236: 217–230.

Vial, J. L. (Ed.) (1973). Evolutionary Biology of the Anurans.

Vences, M., Glaw, F., Kosuch, J., Boehme, W., and Veith, M.

University of Missouri Press, Columbia.

(2001). Phylogeny of South American and Malagasy boine Vicario, S., Caccone, A., and Gauthier, J. (2003). Xantusiid “night”

snakes: Molecular evidence for the validity of Sanzinia and lizards: A puzzling phylogenetic problem revisited using likeli-Acrantophis and biogeographic implications. Copeia 2001: hood-based Bayesian methods on mtDNA sequences. Molecu-1151–1154.

lar Phylogenetics and Evolution 26: 243–261.

Vences, M., Kosuch, J., Glaw, F., Bohme, W., and Veith, M.

Vidal, N., and Hedges, S. B. (2002a). Higher-level relationships (2003c). Molecular phylogeny of hyperoliid treefrogs: Bio-of snakes inferred from four nuclear and mitochondrial geographic origin of Malagasy and Seychellean taxa and genes. Comptes Rendus Biologies 325: 977–985.

re-analysis of familial paraphyly. Journal of Zoological Sys-Vidal, N., and Hedges, S. B. (2002b). Higher-level relationships tematics and Evolutionary Research 41: 205–215.

of snakes inferred from four nuclear and mitochondrial Vences, M., Kosuch, J., Rodel, M. O., Lotters, S., Channing, A., genes. Comptes Rendus Biologies 325: 987–995.

Glaw, F., and Bohme, W. (2004). Phylogeography of Ptycha-Vidal, N., and Hedges, S. B. (2004). Molecular evidence for a dena mascareniensis suggests transoceanic dispersal in a terrestrial origin of snakes. Proceedings of the Royal Society widespread African-Malagasy frog lineage. Journal of Bioge-of London Series B-Biological Sciences 271: S226–S229.

ography 31: 593–601.

Vidal, N., and Hedges, S. B. (2005). The phylogeny of squamate Vences, M., Raxworthy, C. J., Nussbaum, R. A., and Glaw, F.

reptiles (lizards, snakes, and amphisbaenians) inferred from (2003b). A revision of the Scaphiophryne marmorata com-nine nuclear protein-coding genes. Comptes Rendus Biology plex of marbled toads from Madagascar, including the 328: 1000–1008.

description of a new species. Herpetological Journal 13: Vidal, N., Azvolinsky, A., Cruaud, C., and Hedges, S. B. (2008).

69–79.

Origin of tropical American burrowing reptiles by transatlan-Vences, M., Raxworthy, C. J., Nussbaum, R. A., and Glaw, F.

tic rafting. Biology Letters 4: 115–118.

(2003a). New microhylid frog (Plethodontohyla) from Mada-Vieites, D. R., Min, M. S., and Wake, D. B. (2007). Rapid diver-gascar, with semiarboreal habits and possible parental care.

sification and dispersal during periods of global warming by Journal of Herpetology 37: 629–636.

plethodontid salamanders. Proceedings of the National Acad-Vences, M., Wahl-Boos, G., Hoegg, S., Glaw, F., Oliveira, E. S., emy of Sciences (USA) 104: 19903–19907.

Meyer, A., and Perry, S. (2007). Molecular systematics of Vieites, D. R., Nieto-Roman, S., Barluenga, M., Palanca, A., mantelline frogs from Madagascar and the evolution of their Vences, M., and Meyer, A. (2004). Post-mating clutch piracy femoral glands. Biological Journal of the Linnean Society in an amphibian. Nature 431: 305–308.

92: 529–539.

Viertel, B., and Richter, S. (1999). Anatomy: Viscera and endo-Vences, M., Wanke, S., Odierna, G., Kosuch, J., and Veith, M.

crines. In Tadpoles: The Biology of Anuran Larvae. R. W.

(2000). Molecular and karyological data on the South Asian McDiarmid and R. Altig (Eds.). Pp. 92–148. University of Ranid genera Indirana, Nyctibatrachus and Nannophrys of Chicago Press, Chicago.

(Anura: Ranidae). Hamadryad 25: 75–82.

Viets, B. E., Ewert, M. A., Talent, L. G., and Nelson, C. E.

Vermeij, G. J. (1982). Unsuccessful predation and evolution.

(1994). Sex-determining mechanisms in squamate reptiles.

American Naturalist 120: 701–720.

Journal of Experimental Zoology 270: 45–56.

Villa, J. (1984). Biology of a neotropical glass frog, Centrole-Vitt, L. J., and Congdon, J. D. (1978). Body shape, reproductive nella fleischmanni (Boettger), with special reference to its effort, and relative clutch mass in lizards: Resolution of a frogfly associates. Milwaukee Public Museum Contributions paradox. American Naturalist 112: 595–608.

in Biology and Geology 55: 1–60.

Vitt, L. J., and Cooper, W. E., Jr. (1985). The evolution of sexual Villa, J. D., and Wilson, L. D. (1990). Ungaliophis, U. continen-dimorphism in the skink Eumeces laticeps: An example of sex-talis, U. panamensis. Catalogue of American Amphibians ual selection. Canadian Journal of Zoology 63: 995–1002.

and Reptiles 480: 1–4.

Vitt, L. J., and Cooper, W. E., Jr. (1986a). Foraging and diet of a Villecco, E. I., Aybar, M. J., Riera, A. N. S., and Sanchez, S. S.

diurnal predator (Eumeces laticeps) feeding on hidden prey.

(1999). Comparative study of vitellogenesis in the anuran Journal of Herpetology 20: 408–415.

amphibians Ceratophrys cranwelli (Leptodactilidae) and Vitt, L. J., and Cooper, W. E., Jr. (1986b). Tail loss, tail color, Bufo arenarum (Bufonidae). Zygote 7: 11–19.

and predator escape in Eumeces (Lacertilia: Scincidae): Villiers, A. (1975). Les Serpents de l'Ouest Africain. 3rd Ed. Les Age-specific differences in costs and benefits. Canadian Nouvelles E

´ ditions Africaines, Dakar.

Journal of Zoology 64: 583–592.

Vincent, S. E., Shine, R., and Brown, G. P. (2005). Does foraging Vitt, L. J., and Cooper, W. E., Jr. (1988). Feeding responses of mode influence sensory modalites for prey detection? A com-broad-headed skinks (Eumeces laticeps) to velvet ants parison between males and female filesnakes (Acrochordus (Dasymutilla occidentalis). Journal of Herpetology 22: arafurae, Acrochordidae). Animal Behavior 70: 715–721.

485–488.

Vinegar, A., Hutchison, V., and Dowling, H. (1970). Metabo-Vitt, L. J., and de la Torre, S. (1996). Guia para la Investigacion lism, energetics, and thermoregulation during brooding of de las Lagartijas de Cuyabeno—A Research Guide to the snakes of the genus Python (Reptilia. Boidae). Zoologica Lizards of Cuyabeno. Centro de Biodiversidad y Ambiente, 55: 19–48.

Pontificia Universidad Cato´lica del Ecuador, Quito, Ecuador.

Vitt, L. J. (1981). Lizard reproduction: habitat specificity and Vitt, L. J., and Goldberg, S. R. (1983). Reproductive ecology of constraints on relative clutch mass. American Naturalist two tropical iguanid lizards: Tropidurus torquatus and Platy-117: 506–514.

notus semitaeniatus. Copeia 1983: 131–141.

Vitt, L. J. (1983). Ecology of an anuran-eating guild of terrestrial Vitt, L. J., and Lacher, T. E., Jr. (1981). Behavior, habitat, diet, tropical snakes. Herpetologica 39: 52–66.

and reproduction of the iguanid lizard Polychrus acutirostris Vitt, L. J. (1985). On the biology of the little known anguid liz-in the Caatinga of northeastern Brazil. Herpetologica 37: ard, Diploglossus lessonae in northeast Brazil. Papeis Avul-53–63.

sos de Zoologia (Sa˜o Paulo) 36: 69–76.

Vitt, L. J. and Pianka, E. R. (Eds.) (1994). Lizard Ecology: His-Vitt, L. J. (1986). Reproductive tactics of sympatric gekkonid torical and Experimental Perspectives. Princeton University lizards with a comment on the evolutionary and ecological Press, Princeton, N.J.

consequences

of invariant clutch size. Copeia 1986: Vitt, L. J., and Pianka, E. R. (2005). Deep history impacts pres-773–786.

ent-day ecology and biodiversity. Proceedings of the Vitt, L. J. (1991). Ecology and life history of the scansorial arbo-National Academy of Sciences

102: 7877–7881.

real lizard Plica plica (Iguanidae) in Amazonian Brazil.

Vitt, L. J., and Pianka, E. R. (2007). Feeding ecology in the nat-Canadian Journal of Zoology 69: 504–511.

ural world. In Lizard Ecology: The Evolutionary Conse-Vitt, L. J. (1992a). Diversity of reproduction strategies among quences of Foraging Mode. S. M. Reilly, L. D. McBrayer, Brazilian lizards and snakes: The significance of lineage and D. B. Miles (Eds.). Pp. 141–172. Cambridge University and adaptation. In Reproductive Biology of South American Press, Cambrdge UK.

Vertebrates. W. C. Hamlett (Ed.). Pp. 135–149. Springer-Vitt, L. J., and Price, H. J. (1982). Ecological and evolutionary Verlag, New York.

determinants of relative clutch mass in lizards. Herpetologica Vitt, L. J. (1992b). Mimicry of millipedes and centipedes by 38: 237–255.

elongate

terrestrial

vertebrates.

National

Geographic

Vitt, L. J., and Zani, P. A. (1996a). Organization of a taxonomi-Reseach and Exploration 8: 76–95.

cally diverse lizard assemblage in Amazonian Ecuador.

Vitt, L. J. (1993). Ecology of isolated open-formation Tropidurus Canadian Journal of Zoology 74: 1313–1335.

(Reptilia: Tropiduridae) in Amazonian lowland rain forest.

Vitt, L. J., and Zani, P. A. (1996b). Behavioural ecology of Tro-Canadian Journal of Zoology 71: 2370–2390.

pidurus hispidus on isolated rock outcrops in Amazonia.

Vitt, L. J., and Avila-Pires, T. C. S. (1998). Ecology of two sym-Journal of Tropical Ecology 12: 81–101.

patric species of Neusticurus (Sauria: Gymnophthalmidae) in Vitt, L. J., and

Zani, P. A. (1996c). Ecology of the South Ameri-the western Amazon of Brazil. Copeia 1998: 570–582.

can lizard Norops chrysolepis (Polychrotidae). Copeia 1996: Vitt, L. J., and Breitenbach, G. L. (1993). Life histories and repro-56–68.

ductive tactics among lizards in the genus Cnemidophorus Vitt, L. J., and Zani, P. A. (1996d). Ecology of the lizard Ameiva (Sauria: Teiidae). In Biology of Whiptail Lizards (Genus Cne-festiva (Teiidae) in southeastern Nicaragua. Journal of Her-midophorus). J. W. Wright and L. J. Vitt (Eds.). Pp. 211–243.

petology 30: 110–117.

Oklahoma Museum of Natural History, Norman, OK.

Vitt, L. J., and Zani, P. A. (1996e). Ecology of the elusive tropi-Vitt, L. J., and Colli, G. R. (1994). Geographical ecology of a cal lizard Tropidurus [=Uracentron] flaviceps (Tropiduridae) neotropical lizard: Ameiva ameiva (Teiidae) in Brazil. Cana-in lowland rain forest of Ecuador. Herpetologica 52: dian Journal of Zoology 72: 1986–2008.

121–132.

Vitt, L. J., and Zani, P. A. (1997). Ecology of the nocturnal lizard Vitt, L. J., Colli, G. R., Caldwell, J. P., Mesquita, D. O., Garda, A. A., Thecadactylus rapicauda (Sauria: Gekkonidae) in the Ama-and Franca, F. G. R. (2007b). Detecting variation in microhabi-zon region. Herpetologica 53: 165–179.

tat use in low-diversity lizard assemblages across small-scale Vitt, L. J., Congdon, J. D., and Dickson, N. A. (1977). Adaptive habitat gradients. Journal of Herpetology 41: 654–663.

strategies and energetics of tail autotomy in lizards. Ecology Vitt, L. J., A

´ vila-Pires, T. C. S., Esposíto, M. C., Sartorius, S. S., 58: 326–337.

and Zani, P. A. (2007c). Ecology of Alopoglossus angulatus Vitt, L. J., Zani, P. A., and Durtsche, R. D. (1995a). Ecology of and A. atriventris in western Amazonia. Phyllomedusa 6: the lizard Norops oxylophus (Polychrotidae) in lowland for-11–21.

est of southeastern Nicaragua. Canadian Journal of Zoology Vogt, R. C., and Flores-Villela, O. (1992). Effects of incubation 73: 1918–1927.

temperature on sex determination in a community of Neo-Vitt, L. J., Zani, P. A., Caldwell, J. P., and Carrillo, E. O.

tropical freshwater turtles in southern Mexico. Herpetologica (1995b). Ecology of the lizard Kentropyx pelviceps (Sauria: 48: 265–270.

Teiidae) in lowland forest of Ecuador. Canadian Journal of Vogt, R. C., and Guzman, S. (1988). Food partitioning in a Neotrop-Zoology 73: 691–703.

ical freshwater turtle community. Copeia 1988: 37–47.

Vitt, L. J., Zani, P. A., and Caldwell, J. P. (1996b). Behavioural Volse, H. (1944). Structure and seasonal variation of the male ecology of Tropidurus hispidus on isolated rock outcrops in reproductive organs of Vipera berus (L.). Spoila Zoologica Amazonia. Journal of Tropical Ecology 12: 81–101.

Musei Huaniensis 5: 1–157.

Vitt, L. J., Avila-Pires, T. C. S., and Zani, P. A. (1996a). Observa-Vorburger, C. (2006). Geographic parthenogenesis: Recurrent tions on the ecology of the rare Amazonian lizard, Enyalius lee-patterns down under. Current Biology 16: R641–643.

chii (Polychrotidae). Herpetological Natural History 4: 77–82.

Voris, H. K. (1985). Population size estimates for a marine snake Vitt, L. J., Zani, P. A., and Avila-Pires, T. C. S. (1997a). Ecol-

(Enhydrina schistosa) in Malaysia. Copeia 1985: 955–961.

ogy of the arboreal lizard Tropidurus (=Plica) umbra in the Voris, H. K., and Karns, D. R. (1996). Habitat utilization, move-Amazonian region. Canadian Journal of Zoology 75: ments, and activity patterns of Enhydris plumbea (Serpentes: 1876–1882.

Homalopsinae) in a rice paddy wetland in Borneo. Herpeto-Vitt, L. J., Zani, P. A., and Barros, A. A. M. (1997b). Ecological logical Natural History 4: 111–126.

variation among populations of the gekkonid lizard Gona-Voris, H. K., and Voris, H. H. (1983). Feeding strategies in todes humeralis in the Amazon Basin.

Copeia 1997: 32–43.

marine snakes: An analysis of evolutionary, morphological, Vitt, L. J., Avila-Pires, T. C. S., Caldwell, J., and Oliveira, behavioral and ecological relationships. American Zoologist V. R. L. (1998a). The impact of individual tree harvesting 23: 411–425.

on thermal environments of lizards in Amazonian rain forest.

Voris, H. K., and Voris, H. H. (1995). Commuting on the tropical Conservation Biology 12: 655–663.

tides: the life of the yellow-lipped sea krait. Ocean Realm Vitt, L. J., Sartorius, S. S., Avila-Pires, T. C. S., and Espośito, 1995: 57–61.

M. C. (1998b). Use of time, space, and food by the gym-Vorobyeva, E. I. (Ed.) (1994). The Siberian Newt (Salamandrella nophthlamid lizard Prionodactylus eigenmanni from the keyserlingii Dybowski, 1870). Zoogeography, Systematics, western Amazon of Brazil. Canadian Journal of Zoology Morphology. Nauka, Moscow. [in Russian].

76: 1681–1688.

Vorobyeva, E. I. (Ed.) (1995). The Siberian Newt (Salamandrella Vitt, L., Zani, P., and Espośito, M. C. (1999). Historical ecology keyserlingii Dybowski, 1870). Ecology, Behavior, Conserva-of Amazonian lizards: Implications for community ecology.

tion. Nauka, Moscow. [in Russian].

Oikos 87: 286–294.

Vorobyeva, E., and Schultze, H.-P. (1991). Description and sys-Vitt, L. J., Sartorius, S. S., Avila-Pires, T. C. S., and Espośito, tematics of panderichthyid fishes with comments on their M. C. (2001). Life at River's Edge: Ecology of Kentropyx relationship to tetrapods. In Origins of the Higher Groups altamazonica in the Brazilian Amazon. Canadian Journal of Tetrapods. Controversy and Consensus. H.-P. Schultze of Zoology 79: 1855–1865.

and L. Trueb (Eds.). Pp. 68–109. Comstock Publishing Vitt, L. J., Pianka, E. R., Cooper, W. E., and Schwenk, K. (2003).

Associates, Ithaca, NY.

History and the global ecology of squamate reptiles. Ameri-Vrijenhoek, R.

C., Dawley, R. M., Cole, C. J., and Bogart, J. P.

can Naturalist 162: 44–60.

(1989).

A

list

of

the

known

unisexual

vertebrates.

Vitt, L. J., Caldwell, J. P., Sartorius, S. S., Cooper, W. E., Baird, In Evolution and Ecology of Unisexual Vertebrates. R. M.

T. A., Baird, T. D., and Perez-Mellado, V. (2005a). Pushing Dawley and J. P. Bogart (Eds.). Pp. 19–23. New York State the edge: Extended activity as an alternative to risky body Museum, Albany, NY.

temperatures in a herbivorous teiid lizard (Cnemidophorus Wager, V. A. (1986). Frogs of South Africa. Their Fascinating Life murinus: Squamata). Functional Ecology 19: 152–158.

Stories. 2nd edition. Delta Books, Craighall, South Africa.

Vitt, L. J., Sartorius, S. S., Avila-Pires, T. C. S., Zani, P. A., and Wagner, P. J., Ruta, M., and Coates, M. I. (2006). Evolutionary Esposito, M. C. (2005b). Small in a big world: Ecology of patterns in early tetrapods. II. Differing constraints on avail-leaf-litter geckos in new world tropical forests. Herpetologiable character space among clades. Proceedings of the Royal cal Monographs 137–152.

Society B-Biological Sciences 273: 2113–2118.

Vitt, L. J., Shepard, D. B., Caldwell, J. P., Vieira, G. H. C., Wainwright, P. C., and Bennett, A. F. (1992a). The mechanism Franca, F. G. R., and Colli, G. R. (2007a). Living with your of tongue projection in chameleons. II. Electromyographic food: Geckos in termitaria of Canta˜o. Journal of Zoology, tests of functional hypotheses. Journal of Experimental Biol-London 272: 321–

328.

ogy 168: 1–21.

Wainwright, P. C., and Bennett, A. F. (1992b). The mechanism Biology and Phylogeny of Gymnophiona (Caecilians). J.-M.

of tongue projection in chameleons. II. Role of shape change Exbrayat (Ed.). Pp. 1–37. Science Publishers, Enfield, NH.

in muscular hydrostat. Journal of Experimental Biology 168: Wake, M. H., and Dickie, R. (1998). Oviduct structure and func-23–40.

tion and reproductive modes in amphibians. Journal of Wainwright, P. C., Kraklau, D. M., and Bennett, A. F. (1991).

Experimental Zoology 282: 477–506.

Kinematics of tongue projection in Chamaeleo oustaleti.

Walker, A. D. (1961). Triassic reptiles from Elgin area: Stagonole-Journal of Experimental Biology 159: 109–133.

pis, Dasygnathus, and their allies. Philosophical Transactions Wakahara, M., and Yamaguchi, M. (2001). Erythropoiesis and of the Royal Society B-Biological Sciences 244: 103–204.

conversion of RBCs and hemoglobins from larval to adult Wallach, V. (1985). A cladistic analysis of the terrestrial Austra-type during amphibian development. Zoological Science 18: lian Elapidae. In Biology of Australasian Frogs and Reptiles.

891–904.

G. Grigg, R. Shine, and H. Ehmann (Eds.). Pp. 223–253.

Wake, D. B., and Dresner, I. G. (1967). Functional morphology Surrey Beatty & Sons, Chipping Norton Pty Ltd., Sydney, and evolution of tail autotomy in salamanders. Journal of Australia.

Morphology 122: 265–306.

Wallach, V. (1993). Presence of a left lung in the Typhlopidae Wake, D. B., and Elias, P. (1983). New genera and a new species (Reptilia: Serpentes). Journal of the Herpetological Associa-of Central American salamanders with a review of the tropi-tion of Africa 42: 32–33.

cal genera (Amphibia, Caudata, Plethodontidae). Contribu-Wallach, V. (1998). The lungs of snakes. In Biology of the Rep-tions in Science (Los Angeles) 345: 1–19.

tilia. Volume 19, Morphology G. C. Gans and A. S. Gaunt Wake, D. B., and Hanken, J. (1996). Direct development in the (Eds.), Pp. 93–295. Society for the Study of Amphibians lungless salamanders: What are the consequences for devel-and Reptiles, Ithaca, NY.

opmental biology, evolution and phylogenesis? International Wallach, V., and Gu¨nther, R. (1997). Typhlopidae vs. Anomale-Journal of Developmental Biology 40: 859–869.

pididae: The identity of Typhlops mutilatus Werner (Reptilia: Wake, D. B., and O

¨ zeti, N. (1969). Evolutionary relationships in Serpentes). Mitt. Zool. Mus. Berlin 73: 333–342.

the family Salamandridae. Copeia 1969: 124–137.

Wallach, V., and Gu¨nther, R. (1998). Visceral anatomy of the Wake, M. H. (1977). The reproductive biology of caecilians: An Malaysian snake genus Xenophidion, including a cladistic evolutionary perspective. In The Reproductive Biology of analaysis and allocation of a new family (Serpentes: Xeno-Amphibians. D. H. Taylor and S. I. Guttman (Eds.).

phidiidae). Amphibia-Reptilia 19: 385–404.

Pp. 73–101. Plenum Press, New York.

Warburg, M. R., Lewinson, D., and Rosenberg, M. (1994). Struc-Wake, M. H. (1978). The reproductive biology of Eleutherodac-ture and function of Salamandra skin and gills. Mertensiella tylus jasperi (Amphibia, Anura, Leptodactylidae), with com-4: 423–452.

ments on the evolution of live-bearing systems. Journal of Warkentin, K. M. (1995). Adaptive plasticity in hatching age: A Herpetology 12: 121–133.

response to predation risk trade-offs. Proceedings of the Wake, M. H. (1980)

response to predation risk trade-offs. Proceedings of the Wake, M. H. (1980). Reproduction, growth, and population National Academy of Sciences (USA) 92: 3507–3510.

structure of the Central American caecilian Dermophis mex-Warkentin, K. M. (2000). Wasp predation and wasp-induced icanus. Herpetologica 36: 244–256.

hatching of red-eyed treefrog eggs. Animal Behaviour 60: Wake, M. H. (1982). Diversity within a framework of constraints: 503–510.

Reproductive modes in the Amphibia. In Environmental Adap-Warkentin, K. M. (2005). How do embryos assess risk? Vibra-tation and Evolution, a Theoretical and Empirical Approach.

tional cues in predator-induced hatching of red-eyed treeD. Mossakowski and G. Roth (Eds.). Pp. 87–106. Gustav frogs. Animal Behaviour 70: 59–71.

Fischer Verlag, Stuttgart.

Warner, D. A., and Shine, R. (2005). The adaptive significance Wake, M. H. (1989). Hyman’s Comparative Vertebrate Anatomy.

of temperature-dependent sex determination: Experimental Third Edition. University of Chicago Press, Chicago.

tests with a short-lived lizard. Evolution 59: 2209–2221.

Wake, M. H. (1992a). Reproduction in caecilians. In Reproductive Warner, D. A., and Shine, R. (2006). Morphological variation Biology of South American Vertebrates. W. C. Hamlett (Ed.).

does not influence locomotor performance within a cohort Pp. 112–120. Springer-Verlag, New York.

of hatchling lizards (Amphibolurus muricatus, Agamidae).

Wake, M. H. (1992b). Biogeography of Mesoamerican caecilians Oikos 114: 126–134.

(Amphibia: Gymnophiona). Tulane Studies in Zoology and Warner, D. A., and Shine, R. (2007). Reproducing lizards modify Botany, Supplementary Publication 1: 321–325.

sex allocation in response to operational sex ratios. Biology Wake, M. H. (1993a). Non-traditional characters in the assess-Letters 3: 47–50.

ment of caecilian phylogenetic relationships. Herpetological Warner, D. A., and Shine, R. (2008). The adaptive significance Monographs 7: 42–55.

of temperature-dependent sex determination in a reptile.

Wake, M. H. (1993b). Evolution of oviductal gestation in amphi-Nature 451: 566–568.

bians. Journal of Experimental Zoology 266: 394–413.

Warner, D. A., Lovern, M., and Shine, R. (2007). Maternal nutri-Wake, M. H. (1998). Cartilage in the cloaca: Phallodeal spicules tion affects reproductive output and sex allocation in a lizard in caecilians (Amphibia: Gymnophiona). Journal of Mor-with environmental sex determination. Proceedings of the phology 237: 177–186.

Royal Society London Series B 274: 883–890.

Wake, M. H. (2006). A brief history of research on gymnophio-Wassarman, P. M. (1987). The biology and chemistry of fertili-nian reproductive biology and development. In Reproductive zation. Science 235: 553–560.

Wassersug, R. (1996). The biology of Xenopus tadpoles. In The Webb, G. J. W., Choquenot, D., and Whitehead, P. J. (1986).

Biology of Xenopus. R. C. Tinsley and H. R. Kobel (Eds.).

Nests, eggs, and embryonic development of Carettochelys Pp. 195–211. Zoological Society of London, London.

insculpta (Chelonia: Carettochelidae [sic]) from northern Wassersug, R. J. (1971). On the comparative palatability of some Australia. Journal of Zoology, London 1B: 521–550.

dry-season tadpoles from Costa Rica. American Midland Webb, G. J. W., Manolis, S. C., and Whitehead, P. J. (1987).

Naturalist 86: 101–109.

Wildlife Management: Crocodiles and Alligators. Surrey Wassersug, R. J. (1972). The mechanism of ultraplanktonic Beatty & Sons, Chipping Norton Pty

Ltd, N.S.W.

entrapment in anuran larvae. Journal of Morphology 137: Webb, G. J. W., Messel, H., and Magnusson, W. (1977). The 279–288.

nesting of Crocodylus porosus in Arnhem Land, northern Wassersug, R. J. (1973). Aspects of social behavior in anuran larvae.

Australia. Copeia 1977: 238–249.

In Evolutionary Ecology of the Anurans. J. L. Vial, (Ed.).

Webb, J. K., and Shine, R. (1997). A field study of spatial ecol-Pp. 273–297. University of Missouri Press, Columbia.

ogy and movements of a threatened snake species, Hoploce-Wassersug, R. J. (1974). Evolution of anuran life cycles. Science phalus bungaroides. Biological Conservation 82: 203–217.

185: 377–378.

Webb, J. K., and Shine, R. (1998). Ecological characteristics of a Wassersug, R. J. (1976). Internal oral features in Hyla regilla threatened snake species, Hoplocephalus bungaroides (Ser-

(Anura: Hylidae) larvae: An ontogenetic study. Occasional pentes, Elapidae). Animal Conservation 1: 185–193.

Papers of the Museum of Natural History, University of Kan-Webb, J. K., Shine, R., and Christian, K. A. (2006). The adaptive sas 49: 1–24.

significance of reptilian viviparity in the tropics: Testing the Wassersug, R. J. (1980). Internal oral features of larvae from eight maternal manipulation hypothesis. Evolution 60: 115–122.

anuran families: Functional, systematic, ecolutionary and eco-Weekes, H. C. (1935). A review of placentation among reptiles with logical considerations. Miscellaneous Publications of the particular regard to the function and evolution of the placenta.

Museum of Natural History, University of Kansas 68: 1–146.

Proceedings of the Zoological Society of London 3: 625–645.

Wassersug, R. J., and Pyburn, W. F. (1987). The biology of the Wegener, A. (1968). The Origin of Continents and Oceans.

pe-ret’ toad, Otophryne robusta (Microhylidae), with special Methuen, London.

consideration of its fossorial larva and systematic relation-Weisrock, D. W., Harmon, L. J., and Larson, A. (2005). Resolv-ships. Zoological Journal of the Linnean Society 91: ing deep phylogenetic relationships in salamanders: Analyses 137–169.

of mitochondrial and nuclear genomic data. Systematic Biol-Wassersug, R. J., Lum, A. M., and Patel, M. J. (1981). An anal-ogy 54: 758–777.

ysis of school structure for tadpoles (Anura: Amphibia).

Weisrock, D. W., Papenfuss, T. J., Macey, J. R., Litvinchuk, Behavioral Ecology and Sociobiology 9: 15–22.

S. N., Polymeni, R., Ugurtas, I. H., Zhao, E., Jowkar, H., Watkins, J. F., Gehlbach, F. R., and Kroll, J. C. (1969). Attrac-and Larson, A. (2006a). A molecular assessment of phyloge-tant-repellant secretions in blind snakes (Leptotyphlops dul-netic relationships and lineage accumulation rates within the cis) and army ants (Neivamyrex nigrescens). Ecology 50: family Salamandridae (Amphibia, Caudata). Molecular Phy-1098–1102.

logenetics and Evolution 41: 368–383.

Watling, D. (1986). Mai Veikau. Tales of Fijian Wildlife. Pri-Weisrock, D. W., Shaffer, H. B., Storz, B. L., Storz, S. R., and vately printed, Suva, Fiji.

Voss, S. R. (2006b). Multiple nuclear gene sequences iden-Watrous, L. E., and Wheeler, Q. D. (1981). The outgroup compari-tify phylogenetic species boundaries in the rapidly radiating son method of character analysis. Systematic Zoology 30: 1–11.

clade of Mexican ambystomatid salamanders. Molecular Watts, P. C., Buley, K. R., Boardman, W., Ciofi, C., and Ecology 15: 2489–2503.

Gibson, O. R. (2006). Parthenogenesis in komodo dragons.

Weiss, S. L. (2001). The effect of reproduction on food intake of Nature 444: 1021–1022.

a sit-and-wait foraging lizard, Sceloporus virgatus. Herpeto-Webb, C., and Joss, J. (1997). Does predation by the fish Gambusia logica 57: 138–146.

holbrooki (Atheriniformes: Poeciliidae) contribute to declin-Weldon, P. J.

(1990). Responses by vertebrates to chemicals ing frog populations? Australian Zoologist 30: 316–324.

from predators. In Chemical Signals in Vertebrates 5.

Webb, G. J. W. (1977). The natural history of Crocodylus poro-D. W. Macdonald, D. Mu¨ller-Schwarze, and S. E. Natynczuk sus. In Australian Animals and Their Environments. H. Mes-

(Eds.). Pp. 500–521. Oxford University Press, Oxford.

sel and S. Butler (Eds.). Pp. 239–312. Shakespeare Head Wells, K. D. (1977). The social behaviour of anuran amphibians.

Press, Sydney.

Animal Behaviour 15: 666–693.

Webb, G. J. W., and Manolis, S. C. (1989). Crocodiles of Austra-Wells, K. D. (1980). Social behavior and communication of a lia. Reed, Chatswood, N.S.W.

dendrobatid frog (Colostethus trinitatis). Herpetologica 36: Webb, G. J. W., and Manolis, S. C. (1993). Crocodiles of Austra-189–199.

lia. Revised Edtion. Reed, Chatswood, N.S.W.

Wells, K. D. (1981). Parental behavior of male and female frogs.

Webb, G. J. W., and Vernon, B. (1992). Crocodile management In Natural Selection and Social Behavior. R. D. Alexander in the People's Republic of China – a review with recom-and D. W. Tinkle (Eds.). Pp. 184–197. Chiron Press, New York.

mendations. In Crocodile Conservation Action (Crocodile Wells, K. D. (1988). The effect of social interactions on anuran Specialist Group, SSC) Pp. 1–27. IUCN, Glands.

vocal behavior. In The Evolution of the Amphibian Auditory Webb, G. J. W., Buckworth, R., and Manolis, S. C. (1983). Cro-System. B. Fritzsch, M. J. Ryan, W. Wilczynski, T. E.

codylus johnstoni in the McKinlay River, N. T. VI. Nesting Hetherington, and W. Walkowiak (Eds.). Pp. 433–454.

biology. Australian Wildlife Research 10: 607–637.

Wiley, New York.

Wells, K. D. (2007). The Ecology and Behavior of Amphibians.

Proceedings of the New Zealand Ecological Society 20: University of Chicago Press, Chicago.

121–130.

Wells, K. D., and Bard, K. M. (1988). Parental behavior of an Whitaker, R., and Basu, D. (1983). The gharial (Gavialis gange-aquatic-breeding tropical frog, Leptodactylus bolivanus.

ticus): A review. Journal of the Bombay Natural History Journal of Herpetology 22: 361–364.

Society 79: 531–548.

Wells, K. D., and Wells, R. A. (1976). Patterns of movement in a White, J. (1976). Reptiles of the Corruna Hills. Herpetofauna 8: population of the slimy salamander, Plethodon glutinosus, 21–23.

with observations on aggregations. Herpetologica 32: Whitear, M. (1977). A functional comparison between the epi-156–162.

dermis of fish and of amphibians. Symposium of the Zoologi-Welsch, H. H., Jr., and Lind, A. J. (1996). Habitat correlates of cal Society of London 39: 291–313.

the southern torrent salamander, Rhyacotriton variegatus Whitfield, S. M., Bell, K. E., Philippi, T., Sasa, M., Bolan˜os, F., (Caudata: Rhyacotritonidae), in northwestern California.

Chaves, G., Savage, J. M., and Donnelly, M. A. (2007).

Journal of Herpetology 30: 385–398.

Amphibian and reptile declines over 35 years at La Selva, Werner, D. I., Baker, E. M., Gonzales, E. C., and Sosa, I. R. (1987).

Costa Rica. Proceedings of the National Academy of Kinship recognition and grouping in hatchling green iguanas.

Sciences (USA) 104: 8352–8356.

Behavioral Ecology and Sociobiology 21: 83–89.

Whitford, W. G. (1973). The effects of temperature on respira-Werner, E. E. (1986). Amphibian metamorphosis: Growth rate, tion in the Amphibia

(1986). Amphibian metamorphosis: Growth rate, tion in the Amphibia. American Zoologist 13: 505–512.

predator risk, and the optimal size at transformation. Ameri-Whitford, W. G., and Bryant, M. (1979). Behavior of a predator can Naturalist 128: 319–341.

and its prey: The horned lizard (Phrynosoma cornutum) and Werner, E. E., Skelly, D. K., Relyea, R. A., and Yurewicz, K. L.

harvester ants (Pogonomyrmex spp.). Ecology 60: 686–694.

(2007a). Amphibian species richness across environmental Whiting, M. J., Dixon, J. R., and Murray, R. C. (1993). Spatial gradients. Oikos 116: 1697–1712.

distribution of a population of Texas horned lizards (Phryno-Werner, E. E., Yurewicz, K. L., Skelly, D. K., and Relyea, R. A.

soma cornutum: Phrynosomatidae) relative to habitat and (2007b). Turnover in an amphibian metacommunity: The prey. Southwestern Naturalist 38: 150–154.

role of local and regional factors. Oikos 116: 1713–1725.

Whiting, M. J., Nagy, K. A., and Bateman, P. W. (2003). Evolu-Werner, Y. (1997). Observations and comments on active forag-tion and maintenance of social status-signaling badges: ing in geckos. Russian Journal of Herpetology 4: 34–39.

Experimental manipulations in lizards. In Lizard Social Werner, Y. L., Okada, S., Ota, H., Perry, G., and Tokunaga, S.

Behavior. S. F. Fox, J. K. McCoy, and T. A. Baird (Eds.).

(1997). Varied and fluctuating foraging modes in nocturnal Pp. 47–82. Johns Hopkins University Press, Baltimore, MD.

lizards of the family Gekkonidae. Asiatic Herpetological Whittier, J. M., and Crews, D. (1987). Seasonal reproduction: Research 7: 153–165.

Patterns and control. In Hormones and Reproduction in West, N. H., and Van Vliet, B. N. (1983). Open-loop analysis of Fishes, Amphibians, and Reptiles. D. O. Norris and R. E.

the pulmocutaneous baroreflex in the toad Bufo marinus.

Jones (Eds.). Pp. 385–409. Plenum Press, New York.

Jones (Eds.). Pp. 383–405. Plenum Press, New York.

American Journal of Physiology - Regulatory, Integrative, Wibbels, T., Bull, J. J., and Crews, D. (1994). Temperature and Comparative Physiology 245: 642–650.

dependent sex determination: A mechanistic approach. Jour-Wever, E. G. (1978). The Reptile Ear. Its Structure and Func-nal of Experimental Zoology 270: 71–78.

tion. Princeton University Press, Princeton.

Wickramasinghe, D. D., Oseen, K. L., and Wassersug, R. J.

Wever, E. G. (1985). The Amphibian Ear. Princeton University (2007). Ontogenetic changes in diet and intestinal morphol-Press, Princeton.

ogy in semi-terrestrial tadpoles of Nannophrys ceylonensis Wevers, E. (1988). Enige opmerkingen over de pijlgifkikker (Dicroglossidae). Copeia 2007: 1012–1018.

Dendrobates parvulus. Lacerta 46: 51–53.

Wiens, J. J. (1999). Phylogenetic evidence for multiple losses of Weygoldt, P. (1976). Beobachtungen zur Biologie und Ethologie a sexually selected character in phrynosomatid lizards. Pro-von Pipa (Hemipipa) carvalhoi Mir. RiB. 1937 (Anura, Pipi-ceedings of the Royal Society of London Series B-Biological dae). Zeitschrift fu¨r Tierpsychologie 40: 80–99.

Sciences 266: 1529–1535.

Weygoldt, P. (1991). Zur Biologie und zum Verhalten von Phyl-Wiens, J. J., and Donoghue, M. J. (2004). Historical biogeogra-lomedusa marginata Izeckshohn & Da Cruz, 1976 im Terrar-phy, ecology and species richness. Trends in Ecology & Evo-ium. Salamandra 27: 83–96.

lution 19: 639–644.

Weygoldt, P., and de Carvalho e Silva, S. P. (1991). Observa-Wiens, J. J., and Hollingsworth, B. D. (2000). War of the igua-tions on mating, oviposition, egg sac formation and develop-nas: Conflicting molecular and morphological phylogenies ment in the egg-brooding frog, Fritziana goeldii. Amphibia-and long-branch attraction in iguanid lizards. Systematic Reptilia 12: 67–80.

Biology 49: 143–159.

Whimster, I. W. (1990). Neural induction of epidermal sensory Wiens, J. J., and Reeder, T. W. (1997). Phylogeny of the spiny organs in gecko skin. In The Skin of Vertebrates. R. I. C.

lizards (Sceloporus) based on molecular and morphological Spearman and P. A. Riley (Eds.). Pp. 161–167. Linnean Soci-evidence. Herpetological Monographs 11: 1–101.

ety of London, London.

Wiens, J. J., and Titus, T. A. (1991). A phylogenetic analysis of Whitaker, A. H. (1968). The lizards of the Poor Knights Islands.

Spea (Anura: Pelobatidae). Herpetologica 47: 21–28.

New Zealand Journal of Science 11: 623–651.

Wiens, J. J., Bonett, R. M., and Chippindale, P. T. (2005). Ontogeny Whitaker, A. H. (1973). Lizard populations on islands with discombobulates phylogeny: Paedomorphosis and higher-level and without Polynesian rats, Rattus exulans (Peale).

salamander relationships. Systematic Biology 54: 91–110.

Wiens, J. J., Engstrom, T. N., and Chippindale, P. T. (2006).

Wilkinson, M. (1992a). The phylogenetic position of the Rhina-Rapid diversification, incomplete isolation, and the “specia-trematidae (Amphibia: Gymnophiona): Evidence from the tion clock” in North American salamanders (Genus Pletho-larval lateral line system. Amphibia-Reptilia 13: 74–79.

don): Testing the hybrid swarm hypothesis of rapid Wilkinson, M. (1992b). On the life history of the caecilian genus radiation. Evolution 60: 2585–2603.

Uraeotyphlus (Amphibia: Gymnophiona). Herpetological Wiens, J. J., Kuczynski, C. A., Duellman, W. E., and Reeder, Journal 2: 121–124.

T. W. (2007a). Loss and re-evolution of complex life cycles Wilkinson, M. (1996). Resolution of the taxonomic status of in marsupial frogs: Does ancestral trait reconstruction mis-Nectocaecilia hyadee (Roze) and a revised key to the genera lead? Evolution 61: 1886–1899.

genera lead? Evolution 61: 1886–1899.

of the Typhlonectidae. Journal of Herpetology 30: 413–415.

Wiens, J. J., Parra-Olea, G., Garcia-Paris, M., and Wake, D. B.

Wilkinson, M. (1997). Characters, congruence and quality: A (2007b). Phylogenetic history underlies elevational biodiver-study of neuroanatomical and traditional data in caecilian sity patterns in tropical salamanders. Proceedings of the phylogeny. Biological Reviews 72: 423–470.

Royal Society B-Biological Sciences 274: 919–928.

Wilkinson, M., and Nussbaum, R. A. (1996). On the phyloge-Wiewandt, T. A. (1982). Evolution of nesting patterns in igua-netic position of the Uraeotyphlidae (Amphibia: Gymno-nine lizards. In Iguanas of the World: Their Behavior, Ecol-phiona). Copeia 1996: 550–562.

ogy, and Conservation. G. M. Burghardt, and A. S. Rand Wilkinson, M., and Nussbaum, R. A. (1997). Comparative mor-

(Eds.). p. 117–149. Noyes Publications, Park Ridge, N.J.

phology and evolution of the lungless caecilian Atretochoana Wilbur, H. M. (1972). Competition, predation, and the structure eiselti (Taylor) (Amphibia: Gymnophiona: Typhlonectidae).

of the Ambystoma-Rana sylvatica community. Ecology 53: Biological Journal of the Linnean Society 62: 39–109.

3–21.

Wilkinson, M., and Nussbaum, R. A. (2006). Caecilian phylog-Wilbur, H. M. (1975a). A growth model for the turtle Chrysemys eny and classification. In Reproductive Biology and Phylog-picta. Copeia 1975: 337–343.

eny of Gymnophiona (Caecilians). J.-M. Exbrayat (Ed.).

Wilbur, H. M. (1975b). The evolutionary and mathematical Pp. 39–78. Science Publishers, Enfield, NH.

demography of the turtle Chrysemys picta. Ecology 56: Wilkinson, M., Loader, S. P., Gower, D. J., Sheps, J. A., and 64–77.

Cohen, B. L. (2003). Phylogenetic relationships of African Wilbur, H. M. (1980). Complex life cycles. Annual Review of caecilians (Amphibia; Gymnophiona): Insights from mito-Ecology and Systematics 11: 67–93.

chondrial rRNA gene sequences. African Journal of Herpe-Wilbur, H. M. (1987). Regulation of structure in complex sys-tology 52: 83–92.

tems: Experimental temporary pond communities. Ecology Wilkinson, M., Richardson, M. K., Gower, D. J., and Oommen, 68: 1437–1452.

O. V. (2002a). Extended embryo retention, caecilian oviparity Wilbur, H. M. (1997). Experimental ecology of food webs: Com-and amniote origins. Journal of Natural History 36: 2185–2198.

plex systems in temporary ponds. Ecology 78: 2279–2302.

Wilkinson, M., Sebben, A., Schwartz, E. N. F., and Schwartz, Wilbur, H. M., and Collins, J. P. (1973). Ecological aspects of C. A. (1998). The largest lungless tetrapod: Report on a sec-amphibian metamorphosis. Science 182: 1305–1314.

ond specimen of Atretochoana eiselti (Amphibia: Gymno-Wilbur, H. M., and Fauth, J. E. (1990). Experimental aquatic phiona: Typhlonectidae) from Brazil. Journal of Natural food webs: Interactions between two predators and two prey.

History 32: 617–627.

American Naturalist 135: 176–204.

Wilkinson, M., Sheps, J. A., Oommen, O. V., and Cohen, B. L.

Wilcox, T. P., Zwickl, D. J., Heath, T. A., and Hillis, D. M.

(2002b). Phylogenetic relationships of Indian caecilians (2002). Phylogenetic relationships of the dwarf boas and a (Amphibia: Gymnophiona) inferred from mitochondrial comparison of Bayesian and bootstrap measures of phyloge-rRNA gene sequences. Molecular Phylogenetics and Evolu-netic support. Molecular Phylogenetics and Evolution 25: tion 23: 401–407.

361–371.

Willi, U. B., Bronner, G. N., and Narins, P. A. (2006). Middle Wild, E. R. (1995). New genus and species of Amazonian micro-ear dynamics in response to seismic stimuli in the Cape hylid frog with a phylogenetic analysis of New World golden mole (Chrysochloris asiatica). Journal of Experimen-genera. Copeia 1995: 837–849.

tal Biology 209: 302–313.

Wiley, E. O. (1981). Phylogenetics. The Theory and Practice of Williams, E.

E. (1950). Variation and selection in the cervical Phylogenetic Systematics. John Wiley & Sons, New York.

central articulations of living turtles. Bulletin of the American Wiley, E. O. (1988). Vicariance biogeography. Annual Review of Museum of Natural History 94: 505–561.

Ecology and Systematics 19: 513–542.

Williams, E. E. (1969). The ecology of colonization as seen in Wiley, E. O., Siegel-Causey, D., Brooks, D. R., and Funk, V. A.

the zoogeography of anoline lizards on small islands. Quar-

(1991). The Compleat Cladist. A Primer of Phylogenetic Pro-terly Review of Biology 44: 345–389.

cedures. University of Kansas Museum of Natural History, Williams, E. E. (1972). The origin of faunas. Evolution of lizard Special Publication 19: 1–158.

congeners in a complex island fauna: a trial analysis. Evolu-Wilhoft, D. C. (1963). Reproduction in the tropical Australian tionary Biology 6: 47–89.

skink, Leiolopisma rhomboidalis. American Midland Natu-Williams, E. E. (1983). Ecomorphs, faunas, island size, and ralist 70: 442–461.

diverse end points in island radiations of Anolis. In Lizard Wilkinson, M. (1989). On the status of Nectocaecilia fasciata Ecology: Studies of a Model Organism. R. B. Huey, E. R.

Taylor with a discussion of the phylogeny of the Typhlonec-Pianka, and T. W. Schoener (Eds.). Pp. 326–370. Harvard tidae (Amphibia: Gymnophiona). Herpetologica 45: 23–36.

University Press, Cambridge, Mass.

Williams, E. E. (1988). A new look at the Iguania. In Proceedings reed frogs (Hyperolius nasutus: Anura, Hyperoliidae). Jour-of a Workshop on Neotropical Distribution Patterns. W. R.

nal of Experimental Biology 97: 335–343.

Heyer and P. E. Vanzolini (Eds.). Pp. 429–486. Academia Bra-Witmer, L. M. (1991). Perspectives on avian origins. In Origins sileira de Cieˆncias, Rio de Janeiro.

of the Higher Groups of Tetrapods. Controversy and Consen-Williams, G. C. (1966). Adaptation and Natural Selection: A sus. H.-P. Schultze and L. Trueb (Eds.). Pp. 427–466. Com-Critique of some Current Evolutionary Thought. Princeton stock Publishing Associates, Ithaca, NY.

University Press, Princeton, NJ.

Witten, G. J. (1993). Family Agamidae. In Fauna of Australia.

Willis, P. M. A. (1997). Review of fossil crocodilians from Aus-Volume 2A. Amphibia & Reptilia. C. J. Gasby, G. J. B. Ross, tralasia. Australian Zoologist 30: 287–298.

and P. L. Beesley (Eds.). Pp. 240–252. Australian Govern-Willis, R. E., McAliley, L. R., Neeley, E. D., and Densmore, L. D.

ment Publishing Service, Canberra.

(2007). Evidence for placing the false gharial (Tomistoma Woinarski, J. C. Z. (1989). The vertebrate fauna of broombush schlegelii) into the family Gavialidae: Inferences from nuclear Melaleuca uncinata vegetation in northwestern Victoria.

gene sequences. Molecular Phylogenetics and Evolution 43: Australian Wildlife Research 16: 217–238.

787–794.

Wone, B., and Beauchamp, B. (2003). Movement, home range, Wilms, T., and Bo¨hme, W. (2000). Revision of the Uromastyx and activity patterns of the horned lizard, Phrynosoma mcal-acanthinura species group, with description of a new species lii. Journal of Herpetology 37: 679–686.

from the central Sahara (Reptilia: Sauria: Agamidae). Zool.

Woolbright, L. L. (1983). Sexual selection and size dimorphism Abh. Staatl. Mus. Tierk. Dresden 51: 73–104.

in anuran Amphibia. American Naturalist 121: 110–119.

Wilson, D. S. (1998). Nest-site selection: Microhabitat variation Woolbright,

L. L. (1991). The impact of Hurricane Hugo on for-and its effects on the survival of turtle embryos. Ecology est frogs in Puerto Rico. Biotropica 23: 462–467.

79: 1884–1892.

Worthy, T. H. (1987). Osteology of Leiopelma (Amphibia: Leio-Wilson, D. S., Mushinsky, H. R., and McCoy, E. D. (1994).

pelmatidae) and descriptions of three new subfossil Leio-Home range, activity, and use of burrows of juvenile gopher pelma species. Journal of the Royal Society of New tortoises in central Florida. U S Fish and Wildlife Service Zealand 17: 201–251.

Fish and Wildlife Research 13: 147–160.

Wright, J. W. (1993). Evolution of whiptail lizards (Cnemido-Wilson, D. S., Nagy, K. A., Tracy, C. R., Morafka, D. J., and phorus). In Biology of Whiptail Lizards (Genus Cnemido-Yates, R. A. (2001). Water balance in neonate and juvenile phorus). J. W. Wright and L. J. Vitt (Eds.). Pp. 27–81.

desert tortoises, Gopherus agassizii. Herpetological Mono-Oklahoma Museum of Natural History, Norman, OK.

graphs 15: 158–170.

Wright, J. W. and Vitt, L. J. (Eds.) (1993). Biology of Whiptail Wilson, E. O., and Bossert, W. H. (1971). A Primer of Popula-Lizards (Genus Cnemidophorus). Oklahoma Museum of Nat-tion Biology. Sinauer Associates, Stamford, CT.

ural History, Norman, OK.

Wilson, J. (2001). A review of the modes of orientation used by Wu, X.-C., Brinkman, D. B., and Russell, A. R. (1996a). A new amphibians during breeding migration. Journal of the Penn-alligator from the Upper Cretaceous of Canada and the sylvania Academy of Sciences 74: 61–66.

relationships

of

early

eusuchians.

Palaeontology

39:

Wilson, L. D., and Porras, L. (1983). The Ecological Impact 351–375.

of Man on the South Florida Herpetofauna. University of Wu, X.-C., Brinkman, D. B., and Russell, A. R. (1997a).

Kansas Musem of Natural History Special Publication 7, Sineoamphisbaena hexatabularis, an amphisbaenian (Dia-Lawrence, KS.

spsida: Squamata) from the Upper Cretaceous redbeds at Winemiller, K. O., and Pianka, E. R. (1990). Organization in nat-Bayan Mandahu (Inner Mongolia, People's Republic of ural assemblages of desert lizards and tropical fishes. Ecolog-China), and comments on the phylogenetic relationships of ical Monographs 60: 27–55.

the Amphisbaenia. Canadian Journal of Earth Sciences 33: Winter, D. A., Zawada, W. M., and Johnson, A. A. (1986). Com-541–577.

parison of the symbiotic fauna of the family Plethodontidae Wu, X.-C., Russell, A. R., and Brinkman, D. B. (1997b). Phylo-in the Ouachita Mountains of western Arkansas. Proceedings genetic relationships of Sineoamphisbaena hexatabularis: of the Arkansas Academy of Science 40: 82–85.

Further considerations. Canadian Journal of Earth Sciences Wirot, N. (1979). The Turtles of Thailand. Siamfarm Zoological 34: 883–885.

Garden, Bangkok, Thailand.

Wu, X.-C., Sues, H. -D., and Dong, Z. -M. (1996b). Sichuanosu-Withers, P. C. (1992). Comparative Animal Physiology. Saunders chus shuhanensis, a new Early Cretaceous protosuchian College Publishing, New York.

(Archosauria: Crocodyliformes) from Sichuan (China), and Withers, P. C. (1998). Urea: Diverse functions of a 'waste' prod-the monophyly of Protosuchia. Journal of Vertebrate Paleon-uct. Clinical and Experimental Pharmacology and Physiol-tology 17: 89–103.

ogy 25: 722–727.

Wynn, A. H., Cole, C. J., and Gardner, A. L. (1987). Apparent Withers, P.

C., and Richards, S. J. (1995). Cocoon formation by triploidy in the unisexual Brahminy blind snake, Rampho-the treefrog Litoria alboguttata (Amphibia: Hylidae): A typhlops braminus. American Museum Novitates 2868: ‘waterproof’ taxonomic tool? Journal of the Royal Society 1–7.

of Western Australia 78: 103–106.

Xavier, F. (1986). La reproduction des Nectophrynoides.

Withers, P. C., Hillman, S. S., Drewes, R. C., and Sokol, O. M.

In Traite´ de Zoologie. Vol XIV, fasc. I-B. Amphibiens. P. P.

(1982). Water loss and nitrogen excretion in sharp-nosed Grasse and M. Delsol (Eds.). Pp. 497–513. Massons, Paris.

Ydenberg, R. C., and Dill, L. M. (1986). The economics of flee-and phylogenetic perspectives. Biochemical Systematics and ing from predators. Advances in the Study of Behavior 16: Ecology 34: 467–477.

229–249.

Zhang, P., Chen, Y. Q., Liu, Y. F., Zhou, H., and Qu, L. H.

Yeomans, S. R. (1995). Water-finding in adult turtles: Random (2003). The complete mitochondrial genome of the Chinese search or oriented behavior? Animal Behaviour 49: 977–987.

giant salamander, Andrias davidianus (Amphibia: Caudata).

Young, B. A. (1988). The cephalic vascular anatomy of three Gene 311: 93–98.

species of sea snakes. Journal of Morphology 196: 195–204.

Zhang, P., Chen, Y. Q., Zhou, H., Liu, Y. F., Wang, X. L., Young, B. A. (1997). On the absence of taste buds in monitor Papenfuss, T. J., Wake, D. B., and Qu, L. H. (2006). Phylog-lizards (Varanus) and snakes. Journal of Herpetology 31: eny, evolution, and biogeography of Asiatic Salamanders 130–137.

(Hynobiidae). Proceedings of the National Academy of Young, J. E.

(Hynobiidae). Proceedings of the National Academy of Young, J. E., Christian, K. A., Donnellan, S., Tracy, C. R., and Sciences (USA) 103: 7360–7365.

Parry, D. (2005). Comparative analysis of cutaneous evapo-Zhao, E., and Adler, K. (1993). Herpetology of China. Society rative water loss in frogs demonstrates correlation with eco-for the Study of Amphibians and Reptiles, Ithaca, NY.

logical habits. Physiological and Biochemical Zoology 78: Zhao, E., Hu, Q., Jiang, Y., and Yang, Y. (1988). Studies on Chi-847–856.

nese Salamanders. Society for the Study of Amphibians and Young, J. E., Tracy, C. R., Christian, K. A., and McArthur, L. J.

Reptiles, Oxford, Ohio.

(2006). Rates of cutaneous evaporative water loss of native Zheng, Y. C., and Fu, J. Z. (2007). Making a doughnut-shaped Fijian frogs. Copeia 2006: 83–88.

egg mass: Oviposition behaviour of Vibrissaphora boringiae Zaher, H. (1994a). Les Tropidopheoidea (Serpentes; Alethinophi-

(Anura: Megophryidae). Amphibia-Reptilia 28: 309–311.

dia) sont-ils reéllement monophyle´tiques? Arguments en Zhu, M., Ahlberg, P. E., Zhao, W. J., and Jia, L. T. (2002).

faveur de leur polyphyle´tisme. Comptes Rendus de l'Academie Palaeontology - First Devonian tetrapod from Asia. Nature des Sciences Paris, Serie III – Sciences de la Vie 317: 471–478.

420: 760–761.

Zaher, H. (1994b). Comments on the evolution of the jaw adduc-Zimmerman, K., and Heatwole, H. (1990). Cutaneous photore-tor musculature of snakes. Zoological Journal of the Linnean ception: A new sensory mechanism for reptiles. Copeia Society 111: 339–384.

1990: 860–862.

Zaher, H. (1999). Hemipenial morphology of the South Ameri-Zug, G. R. (1991). The lizards of Fiji: Natural history and sys-can xenodontine snakes, with a proposal for a monophyletic tematics. Bishop Museum Bulletin in Zoology 2: 1–136

1–130.

Xenodontinae and a reappraisal of colubroid hemipenes. Bul-Zug, G. R., and Mitchell, J. C. (1995). Amphibians and reptiles letin of the American Museum of Natural History 240: of the Royal Chitwan National Park, Nepal. Asiatic Herpeto-1–168.

logical Research 6: 172–180.

Zamudio, K. R., and Greene, H. W. (1997). Phylogeography of Zug, G. R., and Parham, J. F. (1996). Age and growth in leatherback the bushmaster (Lachesis muta: Viperidae): Implications for turtles, Dermochelys coriacea (Testudines: Dermochelyidae): A Neotropical biogeography, systematics, and conservation.

skeletochronological analysis. Chelonian Conservation Biology Biological Journal of the Linnean Society 62: 421–442.

2: 244–249.

Zangari, F., Cimmaruta, R., and Nascetti, G. (2006). Genetic Zug, G. R., and Zug, P. B. (1979). The marine toad, Bufo mari-relationships of the western Mediterranean painted frogs nus: A natural history resumeóf native populations. Smithso-based on allozymes and mitochondrial markers: Evolutionary nian Contributions to Zoology 284: 1–58.

and taxonomic inferences (Amphibia, Anura, Discoglossi-Zweifel, R. G. (1972). Results of the Archbold Expeditions. No.

dae). Biological Journal of the Linnean Society 87: 515–536.

97. A revision of the frogs of the subfamily Asterophryinae, Zardoya, R., and Meyer, A. (1998). Complete mitochondrial family Microhylidae. Bulletin of the American Museum of genome suggests diapsid affinities of turtles. Proceedings of Natural History 148: 411–546.

the National Academy of Sciences (USA) 95: 14226–14231.

Zweifel, R. G. (1985). Australian frogs of the family Microhyli-Zardoya, R., and Meyer, A. (2000). Mitochondrial evidence on dae. Bulletin of the American Museum of Natural History the phylogenetic position of caecilians (Amphibia: Gymno-182: 265–388.

phiona). Genetics 155: 765–775.

Zweifel, R. G. (1986). A new genus and species of microhylid Zardoya, R., and Meyer, A. (2001). On the origin of and phylo-frog from the Cerro de la Neblina region of Venezuela and genetic relationships among living amphibians. Proceedings a discussion of relationships among New World microhylid of the National Academy of Sciences (USA) 98: 7380–7383.

genera. American Museum Novitates 2863: 1–24.

Zeigler, T., and Bo¨hme, W. (1997). Genital structures and mating Zweifel, R. G. (1989). Long-term ecological studies on a popula-biology in squamate reptiles, especially the Platynota, with tion of painted turtles, Chrysemys picta, on Long Island, New comments on systematics. Mertensiella 8: 1–207.

York. American Museum Novitates 2952: 1–55.

Zeng, X. M., Fu, J. Z., Chen, L. Q., Tian, Y. Z., and Chen, X. H.

Zweifel, R. G., and Lowe, C. H. (1966). The ecology of a popu-

(2006). Cryptic species and systematics of the hynobiid sala-lation of Xantusia vigilis, the desert night lizard. American manders of the Liua-Pseudohynobius complex: Molecular Museum Novitates 2247: 1–57.

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Glossary

This glossary does not attempt completeness; rather we include auditory meatus [n] The car canal, either external or internal.

potentially unfamiliar words that are not defined when they first aufwuchs [n] The aquatic community of microorganisms living appear in the text. Abbreviations: adj, adjective; n, noun; pl, on the surface of submerged objects. Aufwuchs form a coat-plural; v, verb.

ing, often slimy, on which numerous animals, such as tadpoles, graze.

Australian See biogeographic realms.

autopod See limb segments.

A

axilla [n], axillary [adj] See body location.

abiotic [adj] All nonliving components of the environment, e.g., weather and geology.

Age-Specific Mortality [n, adj, n] Proportion of individuals in any age group (cohort) that do not survive to reach the next age group.

B

alate [adj] State of having wings; also used as a noun in refer-Bayesian Inference [adj, n] An iterative process in which the ence to the winged, mating stage of ants and termites.

degree of belief in a hypothesis is updated as evidence accu-allele See chromosome.

mulates. Prior probabilities are continually updated, and posterior probabilities are then calculated based on new Allopatric [adj] Refers to species or populations that are geo-evidence. For examples, see http://en.wikipedia.org/wiki/

graphically isolated from one another.

Bayesian_inference.

Allopatric speciation [adj, n] Process by which one species dif-Bidder's organ A band or cap of ovarian tissue on the testis of ferentiates into two or more species as the result of a physical male bufonids.

barrier, such as a river or mountain range. Also referred to as geographic speciation.

biogeographic realms The major divisions of the world's terrestrial areas, based on shared endemism of plants and amniote [n] A tetrapod that arises developmentally from an animals.

amniotic egg, e.g., reptiles, birds, and mammals.

amphicoelous See vertebral structure.

Australian [adj, n] The biogeographic area of New Gui-nea and adjacent islands, and Australia and adjacent amplexus [n], amplex [v], amplectant [adj], amplectic [adj]

islands.

The "copulatory" behavior of frogs in which the male sits on Ethiopian [adj, n] The biogeographic area of Saharan and the female's back and grasps her with his forelimbs; amplexus sub-Saharan Africa and the southern half of the Arabian can be inguinal (forefeet grasping body immediately in front of Peninsula.

hindlimbs), axillary (immediately behind forelimbs), cephalic Gondwana

The southern continent arising from the breakup (on head or neck), straddled (male sits on shoulders of female of Pangaea consisting of the future Antarctica, South while frogs are vertical and sperm flows down the female's America, Africa, Australia, and New Zealand.

back), or glued (male is attached to females back by adhesive Holarctic [adj, n] The biogeographic area composed of the substance). In amplexus, the cloacae of the male and female Nearctic and Palearctic.

are adpressed and sperm and eggs are extruded simultaneously.

Laurasia The northern continent arising from the breakup of Amplexus is absent in some frogs.

Pangaea consisting of the future North America, Green-anamniote [n] A tetrapod that lacks an amniotic egg in its devel-land, and Eurasia.

opment, e.g., amphibians.

Nearctic [adj, n] The biogeographic area of North America anosmic [adj] Unable to smell; absence of the olfactory sense.

including the Mexican Plateau.

Neotropical [adj, n] The biogeographic area of Central anterior [adj] See body location.

America (excluding the Mexican Plateau), South Amer-arciferal [adj] The anuran pectoral girdle architecture with the ica, and the Greater and Lesser Antilles.

epicoracoids of the left and right side fused anteriorly and Oriental [adj, n] Southern Asia, south of the Himalayan free and overlapping posteriorly.

mountains

and

their

east

and

west

neighboring

Herpetology, 3rd Ed.

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Glossary

mountain ranges from the Indus Valley eastward triploid [adj] Possessing three sets of homologous chromo-through southern China and southward to the Seram-somes. Symbol, 3N.

Halmahera seas.

Palearctic [adj, n] The biogeographic area of Europe, Africa clade [n] A group of organisms containing an ancestor and all its north of the Sahara, and Asia north of the Himalayan descendants.

mountains and their east and west neighboring mountain Cladogenesis [n] see Macroevolution.

ranges.

classification

Pangaea The megacontinent of the Paleozoic period containing all the continental blocks that would become our node name or node-based name This classification category present continents. Pangaea began to break up in the name labels a clade stemming from the immediate com-early Mesozoic.

mon ancestor of two or more designated descendants.

sister group [n] The taxon sharing the most recent common biota [n], biotic [adj] All living components of the environment.

ancestor with another taxon. A pair of taxa sharing the bipedal See locomotion.

same common ancestor.

stem name or stem-based name This classification category body location

name labels a clade of all taxa that are more closely related anterior [adj] The front or head end of an animal.

to a specified set of descendants than to any other taxa.

axilla [n], axillary [adj] At the forelimb insertion.

congeners [n], congeneric [adj] Individuals, populations, or distal [adj] Toward the tip of an extremity, i.e., most distant from the body.

species of the same genus.

dorsum [n], dorsal [adj] The top or upper surface of an ani-conspecifics [n], conspecific [adj] Individuals or populations of mal.

the same species.

inguen [n], inguinal [adj] At the hindlimb insertion.

crèche [n] Nest chamber.

lateral [adj] The side of an animal.

posterior [adj] The rear or tail end of an animal.

proximal [adj] Toward the origin of an extremity, i.e., closest to the body.

D

venter [n], ventral [adj] The underside or lower surface of deme See population.

an animal.

detritovore See diet.

development

direct A developmental pattern in which an egg hatches into C

a miniature adult body form; no larval stage occurs and carnivore See diet.

development is complete or nearly so prior to hatching.

Carolina Bay [adj, n] These ponds form in elliptical depressions indirect A developmental pattern in which an egg hatches and are distributed across the Atlantic seaboard states. They into a larva; the larva is free-living and grows and devel-are typically rich in amphibians and reptiles. see http://en.

ops further prior to metamorphosing into a miniature wikipedia.org/wiki/Carolina_bays for more details.

adult body form.

chromosomes

diet

alleles [n] The different forms of a gene occurring at the carnivore [n], carnivorous [adj] A flesh-eating organism.

same position on different, homologous chromosomes.

detritovore [n], detritivorous [adj] A detritus-eating organ-diploid [adj] Possessing the typical number of chromosomes ism.

following the fusion of the sperm and ovum pronuclei, i.

durophagous [adj] Eating hard-bodied prey; often used in e., a pair each of homologous chromosomes is present.

herpetology for snakes and lizards preying on skinks or Symbol, 2N.

related lizards armored with osteoderms beneath scales.

haploid [adj] Possessing one-half of the homologous chro-folivore [n], folivorous [adj] A foliage-eating organism.

mosomes; the condition obtained by meiotic division to frugivore [n], frugivorous [adj] A fruit-eating organism.

produce sex gametes. Symbol, 1N.

herbivore [n], herbivorous [adj] A plant-eating organism.

heterozygosity [n], heterozygous [adj] The genetic state in insectivore [n], insectivorous [adj] An insect-eating organ-which two different alleles occur at the same position ism, although commonly used for eating any arthropod.

or locus on homologous chromosomes.

molluscivore [n], molluscivorous [adj] A mollusk-eating homozygosity [n], homozygous [adj] The genetic state in organism.

which two identical alleles occur at the same position nectivore [n], nectivorous [adj] A nectar-eating organism.

or locus on homologous chromosomes.

omnivore [n], omnivorous [adj] An organism that con-karyotype [n], karyotypic [adj] The chromosome set of an sumes a variety of plant and animal matter.

organism and its structural characteristics organism and its structural characteristics.

polyploid [adj] Possessing more than two sets of homolo-diplasiocoelous See vertebral structure.

gous chromosomes.

diploid See chromosomes.

distal See body location.

G

diverse [adj] Having numerous, different aspects, such as body gait See locomotion.

forms, courtship behaviors, or temperature or habitat tolerances.

Geographic speciation [adj, n] See Allopatric speciation.

dorsum See body location.

Gondwana See biogeographic realms.

durophagous [adj] See diet.

grade [n] A group of organisms that possess a similar adaptative level of organization.

H

Ecomorph [n] A predictable morphology based on habitat use.

For example, the twig ecomorph of Anolis lizards is thin-habitus [n] The body shape or form of an organism, i.e., its gen-bodied with a long tail. Unrelated species of Anolis on differ-eral appearance.

ent islands have converged on various ecomorphs.

haploid See chromosomes.

edentate, edentulous [adj] Lacking teeth.

hatchling [n] An animal recently hatched from an egg. The epipodium See limb segments.

duration of the hatchling state is variable, although its end in reptiles might be fixed by the disappearance of the Ethiopian See biogeographic realms.

yolk-sac scar.

exaptation [n] A structure, behavior, or physiological feature of heliophilic [adj] Sun-loving.

an organism that serves one function in an ancestor but serves a new and different function in a descendant. A heliothermic [adj] Deriving heat from the sun.

replacement word for the situation previously called pre-herbivore See diet.

adaptation.

heterozygosity See chromosome.

exostosis [n] The condition of a bone having a rugose surface, Holarctic See biogeographic realms.

commonly arising from the fusion of bone and dermis or osteoderms.

holochordal See vertebral structure.

extant [adj, n] The state of a population or species of being alive homozygosity See chromosome.

now; not extinct.

hydroperiod [n] A cycle characterized by a period of dryness; often used in amphibian biology in reference to the period when an ephemeral pond has water.

F

fertilization [n] The penetration of the ovum’s cell membrane by the sperm and the fusion of the sperm and ovum pronuclei to I

reestablish a diploid state.

inguen [n], inguinal [adj] See body location.

external The condition when the sperm and ovum come in insectivore See diet.

contact external to the reproductive tract or cloaca of a female.

internal The condition when the sperm and ovum come in contact within the reproductive tract or cloaca of a K

female.

karyotype See chromosomes.

firmisternal [adj] The anuran pectoral girdle architecture with the left and right epicoracoids fused anteriorly and posteriorly.

folivore See diet.

fossorial [adj] Living underground; not all fossorial animals L

are burrowers but instead may use preexisting holes and lateral See body location.

cavities in the earth.

Laurasia See biogeographic realms.

frugivore See diet.

limb segments

Fertility Rate [adj, n] The average number of offspring that an organism can produce in its lifetime. Fertility rate is cal-autopod [n] The distal part of the limb, including the meso-culated by summing the average number of offspring propodium, metapodium, and the phalanges.

duced at each age. For example, a turtle might produce epidpodium [n], epipodial [adj] The second segment of the 10 eggs at age 1, 30 at age 2, 35 at age 3, and so on.

limb, including either the radius and ulna or the tibia and See also “net reproductive rate.”

fibula. Zeugopod is a synonym.

Glossary

mesopodium [n] The third segment of the limb, including monoestrous [adj] Having a single gametogenic cycle within a either the wrist bones (carpus) or the ankle bones (tar-single reproductive season. See also polyestrous.

sus).

monophyly [n], monophyletic [adj] A taxonomic group whose metapodium [n] A distal segment of the limb, including members share the same ancestor. See also clade, paraphyly, either the metacarpal or the metatarsal elements.

and polyphyly.

propodium [n], propodial [adj] The most proximal segment of the limb, including either the humerus or the femur.

morph [n] A particular body form or colored group of indivi-Stylopod is a synonym.

duals. Morph is used regularly in discussion of polymorphism and variation of individuals within a population or species.

locomotion

morphology [n], morphological [adj] The study of an organ-bipedal [adj] Moving on two limbs.

ism’s form or shape, or the shape of one or more of an organ-gait [n] The pattern of limb movement.

ism’s parts.

quadrupedal [adj] Moving on four limbs.

rectilinear locomotion [n] A mode of limbless locomotion dependent upon a wavelike pattern of rib movement to move the animal forward.

N

saltatory [adj] Moving by jumping, either bipedally or quad-Nearctic See biogeographic realms.

rupedally.

nectivore See diet.

serpentine [adj] A mode of limbless, undulatory locomotion in which all portions of the body pass along the same neonate [n] An animal recently born, i.e., it has emerged from path and use the same frictional surfaces for pushing the female’s reproductive tract.

the body forward.

Neotropical See biogeographic realms.

sidewinding [adj] A specialized mode of serpentine locomotion in which only two parts of the body touch the ground Net Reproductive Rate [adj, adj, noun] Number of offspring pro-simultaneously.

duced by a female during its lifetime taking into consideration not only the fertility rate, but also age-specific mortality rates.

undulatory [adj] A group of limbless locomotion patterns in which the body moves through a series of curves.

nictitating membrane Same as palpebral membrane.

node-based names See classification.

notochordal See vertebral structure.

M

Macroevolution [n] Any evolutionary change occurring at or O

above the species level. At the very least, macroevolution omnivore See diet.

results in the splitting of one species into two. The splitting of one species into two or the splitting of higher order clades opisthocoelous See vertebral structure.

is often called cladogenesis.

Oriental See biogeographic realms.

manus [n] Hand or forefoot.

oviposit [v] To lay eggs.

meiosis [n], meiotic [adj] Gametic cell division in which the number of chromosomes in a sex cell is halved.

mesic [adj] Habitat with moderate moisture level or water availability; adapted to moist conditions.

P

palpebral membrane [n] A transparent “eyelid” that lies Mesoamerica [n] The portion of Central America from central beneath the true eyelids and can extend horizontally from Mexico to Nicaragua.

its resting position in the inner corner of the eye to the outer mesopodium See limb segments.

corner.

metapodium See limb segments.

Palearctic See biogeographic realms.

metapopulation See population.

Pangaea See biogeographic realms.

Microevolution [n] Evolution that results from small changes in panmixis [n], panmictic [adj] Random and unrestricted mating allele frequencies within a population. It occurs below the within a population, thereby allowing the interchange of species level.

genes among all parts of a population.

mitosis [n], mitotic [adj] Regular, nongametic cell division in paraphyly [n], paraphyletic [adj] A taxonomic group contain-which each homologous chromosome duplicates itself; ing most but not all taxa derived from the same ancestor.

when the cell and nucleus divide, the sister cells retain their See also monophyly and polyphyly.

original ploidy or number of chromosomes.

perennibranchiate [adj] The retention of external (larval) gills molluscivore See diet.

as an adult.

periphyton [n] A synonym of aufwuchs; see above.

saltatory See locomotion.

pes [n] Foot, specifically the hindfoot.

saxicolous [adj] Living on or among rocks.

pheromone [n] A chemical signal secreted by one animal that serpentine See locomotion.

conveys specific information to another animal, usually a sidewinding See locomotion.

conspecific, and often elicits a specific behavioral and/or physiological response.

sister group See classification.

Philopatry [n] Refers to individual animals that return to a spe-speciose [adj] A taxon with many species.

cific location, usually to breed or feed.

spermatheca [n] A chamber for storing spermatozoa, usually phylogenesis [n], phylogenetic [adj] The evolutionary history of multibranched, in the wall of some female salamanders.

a taxon.

spermatophore [n] A mucoid pedestal to support the sperm phytotelma, phytotelmata [pl, n] Small bodies of water within packets of some male salamanders; it is produced in the or on plants, e.g., pools in bromeliads.

cloaca.

polyestrous [adj] Having two or more gametogenic cycles stegochordal See vertebral structure.

within a single reproductive season. See also monoestrous.

stem name See classification.

polyphyly [n], polyphyletic [adj] A taxonomic group whose supraciliary

[adj] Above the eye; eyebrow area.

members do not share the same ancestor. See also grade, SVL [n] Snout-vent length; straight-line distance from the tip of monophyly, and paraphyly.

the snout to the anterior edge of the vent.

polyploid See chromosomes.

Sympatric [adj] Refers to species or populations that occur population

together in the same geographic area.

deme [n] A small local population, panmictic in concept if Sympatric Speciation [adj., n] Refers to a process by which a not in actuality.

species differentiates into two or more species with no phys-metapopulation [n] A population of several to many smaller ical barriers isolating the populations.

populations or demes in the same geographic area; the smaller populations potentially exchange members by migration.

population [n] All individuals of the same species within a prescribed area.

T

posterior See body location.

taxon, taxa [pl, n] All members of a taxonomic group of organisms, e.g., Anolis, all members of all species classified in this postmetamorph [n] An amphibian that has recently completed metamorphosis, or the entire life stage following metamor-particular genus.

phosis, in contrast to the larval or premetamorphic stage.

tectorial membrane [n] A membrane in the inner ear covering a patch of sensory hairs.

primitive [adj, n] A character or condition that is the same as an ancestral character or condition.

TL [n] Various; used for Tail Length or Total Length. For tail length, it is distance from posterior edge of the vent to the procoelous See vertebral structure.

tip of the tail, and for total length, distance from tip of snout propodium See limb segments.

to tip of tail.

proximal See body location.

trackway [n] A fossilized trail of footprints.

triploid See chromosomes.

tympanum, tympana [pl, n] Eardrum.

Q

quadrupedal See locomotion.

U

undulatory See locomotion.

R

urticating hairs [n] Defensive hairlike structures that break off rectilinear locomotion See locomotion.

the surface of an organism and cause irritation to the attack-rupicolous [adj] Living on walls or rocks.

ing herbivore or predator.

V

salps [n, pl] Free-swimming, oceanic tunicates in the genus venter, ventral See body location.

Salpa with transparent, fusiform bodies.

vertebral structure

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Glossary

amphicoelous [adj] A vertebra in which the centrum is con-stegochordal [adj] Structurally, a flattened centrum in which cave on both the anterior and the posterior surface.

only the dorsal portion of the notochordal sheath has diplasiocoelous [adj] The condition of the vertebral column ossified.

with seven procoelous presacral vertebrae, the eighth presacral vertebra is biconcave, and the sacral vertebra is X

biconvex posteriorly.

xeric [adj] Habitat with low moisture level or water availability; holochordal [adj] Structurally, a centrum in which the noto-adapted to dry or arid conditions.

chord has been totally replaced.

notochordal [adj] Structurally, a centrum in which a small remnant of the notochord remains in the center of the REFERENCES

centrum.

opisthocoelous [adj] A vertebra in which the centrum is con-Lincoln, R. J., *et al.* (1982). “A Dictionary of Ecology, Evolution and vex on the anterior surface and concave on the posterior Systematics.” Cambridge Univ. Press, Cambridge.

surface.

Lincoln, R. J., and Boxshall, G. A.(1987). “The Cambridge Illustrated procoelous [adj] A vertebra in which the centrum is concave Dictionary of Natural History.” Cambridge Univ. Press, Cambridge.

on the anterior surface and convex on the posterior sur-Peters, J. A. (1964). “Dictionary of Herpetology.” Hafner Publ. Co., New face.

York.

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