Biology and Conservation of Horseshoe Crabs
John T. Tanacredi · Mark L. Botton · David R. Smith
Editors

Biology and Conservation of Horseshoe Crabs

Foreword by Sylvia A. Earle

Springer
We dedicate this book to Drs. Carl N. Shuster, Jr. and Koichi Sekiguchi for their life-long contributions to the biology and conservation of the magnificent horseshoe crab.
Horseshoe crabs, those mysterious ancient mariners, lured me into the sea as a child along the beaches of New Jersey. Drawn to their shiny domed shells and spiked tails, I could not resist picking them up, turning them over and watching the wondrous mechanical movement of their glistening legs, articulating with one another as smoothly as the inner working of a clock.

What was it like to be a horseshoe crab, I wondered? What did they eat? Did they always move around together? Why were some so large and others much smaller? How old were they, anyway? What must it feel like to live underwater? What else was out there, down there, in the cool, green depths that gave rise to such intriguing creatures? The only way to find out, I reasoned, would be to go into the ocean and see for myself, and so I did, and more than 60 years later, I still do.

When Dr. John Tanacredi, perhaps the horseshoe crab’s best friend, invited me to come to Dowling College to participate in the first international conference about these “living fossils,” I was pleased to join more than 150 scientists from 10 countries to explore the past, present, and future of the creatures that have inspired in all who attended an unabashed admiration, relentless curiosity, and growing concern about their recent sharp decline. All of us not only learned from our shared experiences, but were thrilled and deeply inspired by the many youngsters whose artistic interpretations of the life and times of horseshoe crabs were displayed at the conference.

Excitement at the conference about new discoveries was tempered by an undercurrent of concern about the possible loss of the four species of horseshoe crabs presently maintaining a tenuous hold on life in parts of the Atlantic, Pacific, and Indian oceans. They are, after all, symbols of survival on a geological scale. Fossil remains of species from four million centuries ago appear remarkably similar to the craggy, golden-brown animals that now clamber high on moist, sandy beaches to deposit masses of eggs on the tides of early summer.

Gone are the ammonites, the trilobites, and numerous other once abundant creatures with whom they shared ancient oceans. The Atlantic Ocean has opened, closed, and formed again during their time. Ice ages have come and gone as the planet repeatedly cooled, warmed, and cooled again. Horseshoe crabs were witnesses to the arrival and departure of great ocean-dwelling
reptiles and terrestrial dinosaurs and remained through waves of extinction and of numerous new arrivals: insects, spiders, birds, mammals, salamanders and frogs, trees, flowers, and eventually, Homo sapiens.

If a population of living pterodactyls or Tyrannosaurus rex turned up alive and well in some remote part of the planet, it is likely that supreme efforts would be mobilized to protect them while we took advantage of the opportunity to gain new insights about them, and through them, something about the nature of life as it was during the Jurassic Era. Horseshoe crabs preceded such creatures by many millions of years and miraculously, some of them are still around. With living creatures rather than fossilized remains, we have a chance to discover something of the origins of various other life forms, learn secrets of survival during major shifts in planetary temperature, chemistry, food webs, and much more.

The four species of horseshoe crabs, the only living representatives of an entire Class of organisms, have already provided scientists with a window into the past as well as yielding valuable insight concerning the chemistry of life, the nature of vision, and some of the intricacies of nervous system development. Their unique blood, eyes, genetic material, and basic structure continue to provide priceless knowledge that far outweighs their value when killed as a commodity. Direct predation by people, incidental killing of large numbers trapped in nets and trawls, and vast depletion of their shoreline habitats, from beaches to productive offshore waters, have combined in the past few decades to threaten these amazingly durable animals with extinction.

There is time, but not a lot, to take actions to protect these venerable but vulnerable animals. Under the UNESCO World Heritage Program, it may be possible to win support for horseshoe crabs as the first “World Heritage Species.” Designating protected areas along critical coastal nesting areas would certainly help, as well as providing rational guidelines for when and how – and how many – might be extracted for scientific, medical, or other uses. It will be difficult to explain to future generations that we valued these amazing creatures more for use as bait and fertilizer than we did as an on-going source of knowledge – and inspiration.

If for no other reasons, it makes sense to protect these amazing animals out of respect for what they represent as planetary “elders.” Having endured so much for so long, it would be a terrible legacy for humankind if the horseshoe crabs’ astonishingly capacity for survival would come to an end on our watch.

The 2007 International Horseshoe Crab Conference and this volume are promising signs that knowing leads to caring, and with caring, there is hope that horseshoe crabs – and humankind – will share an enduring future.

Sylvia A. Earle
Preface

In this book, you will find the proceedings of a ground-breaking international symposium on the science and conservation of a remarkable group of living species, the horseshoe crab. Earth has only four extant horseshoe crabs: Limulus polyphemus in North America; Tachypleus tridentatus; T. gigas; and Carcinoscorpius rotundicauda in southeast Asia. In past decades, these animals were viewed as a natural history curiosity at best or reviled as enemies of shellfish. Today, we know them as flagship species and invaluable to human health. Their blood provides a chemical known as Limulus amebocyte lysate or LAL that clots in the presence of minute quantities of bacterial endotoxin and is used to ensure that pharmaceuticals and surgical implants are free of bacterial contamination. Current research points to the promise of horseshoe crab blood in the discovery of new treatments for human disease. Horseshoe crabs are integral to the food web of coastal marine ecosystems and to the economies of coastal communities.

Horseshoe crabs are well known as “living fossils” with a geological history covering hundreds of millions of years and an ancestry reaching back 455 million years to the doorstep of the Cambrian. In spite of this longevity, each species now faces common and growing threats to their survival. Loss of essential spawning habitat due to erosion and shoreline development, coastal pollution, and overfishing all threaten horseshoe crab populations. Biologists and conservationists working in coastal areas throughout North America and Southeast Asia have become increasingly concerned by declines observed in all species of horseshoe crab. A consensus emerged that a structured forum was needed where those working on horseshoe crab conservation could meet, exchange ideas, and plan future research and conservation strategies. In the fall of 2005, a planning committee was formed and selected Dowling College to host the first International Symposium on the Science and Conservation of Horseshoe Crabs (ISSCHC 07).

The symposium, which was held during June 11–14, 2007, brought together a diverse group of researchers, ecologists, managers, and educators who took full advantage of the rare opportunity to interact. Participants included biologists who discover processes underlying behavior and population dynamics, medical researchers who mine deep into the pharmaceutical applications, resource
managers who work to ensure healthy and viable populations, and educators
who creatively share fascinating details about horseshoe crabs with the broader
public and future generations. Those at the symposium were enlightened by the
display of children’s art work from around world organized by ERDG, a non-
profit organization. The display reminded the attendees of their own youthful
excitement as they first encountered and explored these alien-looking creatures.

In addition to its many ecological roles, the horseshoe crab is an interna-
tional ambassador. The global distribution of the four horseshoe crab species
links the eastern and western hemispheres. The symposium logo designed by
Dr. Carl N. Shuster Jr. reflects this interconnectedness by showing the two
hemispheres and the four species side-by-side facing the same future. And so it
was at the symposium, where participants from around the world gathered to
share knowledge, present research results, and identify conservation challenges
facing horseshoe crabs. Over 150 scientists, researchers, and students from 10
countries presented over 45 papers and 40 posters. And it is in the pages of this
book where that shared international knowledge and experience is presented as
a beginning in our collective efforts to conserve the world’s horseshoe crab
species.

Science helping to advance conservation; Conservation helping to prioritize
science was chosen as the symposium theme to emphasize that effective con-
servation depends on science-based resource management. Using biological
knowledge as a foundation, populations can be effectively conserved through
management of habitat and human use. This theme of bridging biological
science and conservation served to guide the symposium program and the
organization in this book.

This book is organized, as the title implies, into two main sections: Biology and
Conservation. The Biology section is divided into two subsections: (1) Populations
and Habitats and (2) Physiology, Reproduction, and Development. The Conserv-
ation section is divided into three subsections: (1) Commercial Use and Manage-
ment of Populations and Habitat, (2) Culture and Captive Breeding, and (3) Public
Awareness and Community-based Conservation. Throughout the book, the
reader will find results of new studies, and authoritative reviews on the science
and conservation of all four of the world’s horseshoe crab species. The chapters in
this book were drawn from the invited oral presentations at the symposium, with a
number of additional chapters chosen from among the contributed poster pre-
sentations to achieve greater balance among topics or geographic regions.

During the symposium, a petition with over 200 signatures was prepared to
be given to the Director of UNESCO asking that the very first officially
designated “World Heritage Species,” an invertebrate, be assigned to “Horse-
shoe Crabs” to afford them added protection and awareness, under the World
Heritage Program of the United Nations.

The Editors gratefully acknowledge the work and contributions of our fellow
members of the ISSCHC 07 Planning Committee: Jim Berkson, Jane Brockmann,
Ruth Carmichael, Anil Chatterji, Chang-Po Chen, Annie Christianus, Glenn
Gauvry, Tomio Itow, Jack Levin, Mike Millard, Mike Oates, Martin Schreibman,
Carl Shuster, and Jaime Zaldivar-Rae. Glenn Gauvry and Mariko Sai helped to encourage the participation of many of the attendees from southeast Asia, and they were extremely helpful in coordinating the submission and review of their manuscripts. Dowling College with the Great South Bay in its backyard provided a welcoming facility for the first, of what we hope will be many, International Symposia on the Science and Conservation of Horseshoe Crabs. Communication among symposium attendees was greatly facilitated by the expert translation services provided by Andrew Meehan-Migita and associate. Valerie Royall graphically designed the symposium logo based on Carl Shuster’s conceptual drawing. We also thank Drs. Gregory Lewbart, Cheryl Morrison, Meredith Bartron, and Bob Loveland for their helpful manuscript reviews. MLB is grateful to Fordham University for providing him with a Faculty Fellowship during the fall 2007 semester, when much of the preparation of this book took place. DRS is grateful to USGS Leetown Science Center for administrative support during the planning of the symposium.

JTT extends very special thank you to Ms. Traci D’Alessio, the Dowling College HSC Conference Coordinator and Graduate Assistant whose patience, professionalism and organizational skills were instrumental in making this conference such a success; others at Dowling College that we extend a special thank you to are Tom Franz, Charles McCabe, Roxann Hristovsky from the IT Division for their expert assistance; Lou Siegel, Erik Paulson, Dr. Linda Ardito, Dr. Paul Abramson, Dr. Yu-wan Wang, the Director of International student services at Dowling College whose abundant grace and intelligence, provided invaluable travel and translation service to the international participants, Ms. Henna M. Wang, the Dowling Institute (Horseshoe Crab Central), Sixto Portilla, Lauren Macri, Deborah Wynne, Maria Lovejoy, Tom Downs, Mark Carattini, Food Services by Lessings Inc., volunteers, Joanne Cardinali, Jeannine Lyn Orlando, and Dowling College Earth and Environmental Science students, Farah LaRonde, Sherri Eisenberg and Russell Ainbinder; all whose help made this conference and its proceedings possible JTT would also care to extend a heartfelt “thank you” to New York State Assemblywoman Ginny Fields who continuously supported the efforts to preserve and protect horseshoe crab habitat and populations on Long Island.

Lastly, the Editors wish to extend our heartfelt thanks to the publishers of this work, Springer, Ltd. most notable to Melinda “Lindy” Paul who got this off the ground and to Janet Slobodien who has through her guidance, foresight, review, and overall support has allowed these proceedings to be completed. As with any such undertaking, mistakes or omissions are ours only to bear.

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A few words . . .

One of my first official acts as President of Dowling College was to greet the participants in the International Symposium on the Science and Conservation of Horseshoe Crabs (ISSCHC) 2007 Conference held on the Dowling campus.

Throughout my professional career, whether as an elected official, practicing attorney, or President of an academic institution, I have been guided by the maxim of the Nobel Laureate Rene Dubos: “Think globally; act locally.” The ISSCHC-07 Conference brought that concept to fruition. Our campus hosted scientists, students, and concerned individuals from around the world – a truly global event.

I would like to offer a special note of appreciation to Dr. John Tanacredi, Chair of the Department of Earth and Marine Sciences at Dowling College, and member of the ISSCHC-07 planning committee whose initiative brought the conference to the Dowling venue. The planning committee valiantly worked to raise the necessary funds to hold this symposium, and their collective energy spawned the participation of some 150 scientists and students from 10 countries.

The international perspective on horseshoe crabs brought home to those of us living on Long Island the need for constant vigilance in order to conserve these amazing animals. If we are to preserve these globally significant species, there must be a continual search for answers to the questions needing attention. I am proud that Dowling has been part of this effort.

President
Dowling College

Robert J. Gaffney
Thank You to the Sponsors of the 2007 International Symposium on the Science and Conservation of Horseshoe Crabs

The ISSCHC 07 Planning Committee expresses their deep appreciation for the sponsors who lent their support through funding or significant in-kind services to make the symposium a great success and make this publication possible. Their support was an active demonstration of commitment to the conservation of the world’s horseshoe crabs.

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Part I
Biology
Fig. 1a The oldest known fossil horseshoe crab, *Lunataspis aurora* and its living relative, *Limulus polyphemus*. (courtesy of D. Rudkin and G. Young)
Limits on the Global Distribution of Horseshoe Crabs (Limulacea): Lessons Learned from Two Lifetimes of Observations: Asia and America

Koichi Sekiguchi and Carl N. Shuster Jr.

Abstract This paper is based on the premise that understanding the natural history and ecology of the horseshoe crabs (Limulacea) is paramount to conservation of the species. Our objective has been to select those large-scale, global parameters that help to define the opportunities for, and the limits on, their distribution. Essentially, we have selected the big-picture type of conditions pertinent to considerations of the conservation of the species. This has led to an examination of potential biotic and environmental parameters. Of these we have selected eight, four in each category. The biotic aspects are: who they are (taxonomically), whether they are living fossils, what they are (ecologically), and the significance of discrete populations in conservation of the species. Four large-scale environmental parameters that limit their global distribution are geologic (estuarine environments, continental shelves as avenues of distribution, ocean deeps as deterrents), temperature which sets boundaries, tidal types that define predominant potential spawning sites, and the influence of benthic currents.

1 Introduction

If understanding horseshoe crabs, their natural history and ecology, is the basis for considering their conservation, then we have accumulated the right background. We have been fortunate in having major scientists as our mentors and access to information compiled by the many scientists that preceded us. We began with studies on developmental stages of horseshoe crabs. Later, research included specimen and data-collecting missions to many Indo-Pacific habitats for three species (Tachypleus tridentatus, T. gigas, and Carcinoscorpius rotundicauda) (KS) and from Dauphin Island, Alabama to Maine, USA (Limulus polyphemus) (CS), and several mutual rendezvous on the shores of Delaware Bay.

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When we began our studies in the 1930s and 1940s, respectively, virtually no one else was broadly interested in their natural history and ecology. Also, we are of the generation of students whose professors expected them to have an understanding of who knew what, where, and when about the subject, and, when pertinent, how and why. From that beginning we also have been fortunate to have witnessed and participated with many others in learning more about horseshoe crabs. For all those reasons, we have had scientifically exhilarating careers; ones that have bridged the gaps between the leaders of yore in the study of horseshoe crabs with those of the present.

2 The Nature of the Limulacea

The Limulacea are an ancient group of aquatic merostome arthropods. Their existence through millions of years with relatively few species, exemplifies their designation as ecological generalists. They inhabit coastal embayments and breed on intertidal shores within global constraints such as the oceanic abyss and certain tidal regimes.

2.1 They Are Ancient

Horseshoe crabs are merostomes, those creatures with their legs arranged around their ventral mouths. They are aquatic grade chelicerates (Shuster and Anderson 2003), closely related to trilobites, that occurred earlier in geologic time than the arachnids. Only a few species of horseshoe crabs have existed during any geological period throughout time (Shuster and Anderson 2003). Their conservative exoskeleton and internal organs (Sekiguchi 1988) date back at least to the Carboniferous Period, 245 million years ago. An older date of 445 million years was reported at this symposium by David Rudkin and later published (Rudkin et al. 2008). The exoskeleton is comprised of three articulating sections: the prosoma (a cephalic/thoracic shield containing most of the organ systems and eight pairs of variously modified legs) that articulates by a piano-type hinge with the opisthosoma (the mid-piece bearing the branchial appendages) from which the long spike-like telson swivels on an almost universal joint (Shuster 2001). In reflecting upon the horseshoe crab body as a machine, it is remarkable that of the many thing it can do it cannot back up – it is unable to reverse its tracks.

Taxonomically the four extant species (Figs. 1 and 2) are assigned to three genera in two families in the Superfamily Limulacea:

Family Limulidae
Limulus polyphemus (Linnaeus)
Family Tachypleinae

*Tachypleus tridentatus* (Leach 1819)
*Tachypleus gigas* (Müller 1785)
*Carcinoscorpius rotundicauda* (Latreille 1802)

Yamasaki (1988) proposed renaming *C. rotundicauda* as *Tachypleus rotundicauda* (Latreille 1802) n. comp. – with which we agree, but this has to be brought to the International Commission on Zoological Nomenclature for adjudication. Meanwhile, *Carcinoscorpius*, an apt descriptor, is in general use.

### 2.2 Are They Living Fossils?

Extant horseshoe crabs have been labeled “living fossils” for a long time. This appellation is not exactly true – there are no known fossils of any of the four extant species. The concept most likely had its basis in the constancy of the typical horseshoe crabs three-piece exoskeleton (prosoma, opisthosoma, and telson) since the mid-Paleozoic Era. This lengthy history makes a strong
positive statement – that the three-piece body architecture did the job millions of years ago and, with minor various, is still performing adequately. Their physiology has changed, however, as indicated by the genetic and habitat differences in populations. The combination of a static body form and an adaptable physiology is what probably enabled xiphosuran species to exist in different environmental conditions during that time span.

Two anatomically well-defined fossilized species illustrate the basic body form: (1) *Limulus coffini* (Fig. 3) – found in a concretion formed some 80 million years ago during the Cretaceous in the shallow seas where Colorado now exists (Reeside and Harris 1952), and (2) *Mesolimulus walchi* (Fig. 4) – preserved in the Solnhofen limestones laid down during the Upper Jurassic in the shallow sea that once covered central Europe about 150 million years ago. If these two species could be restored to their original form, it is unlikely that they would be any more anatomically different from the four extant species than the four are from each other. Indeed, if there were more of the single fossil on which *L. coffini* was based, so that a better identification could be made, it might qualify as an ancient race of *L. polyphemus*. If so, we would have a factual basis for the concept of a “living fossil” – at least for about 80 million years, well within the divergence of the American species from the three Indo-Pacific species 135 million years ago (Shishikura et al. 1982).
2.3 They Are Environmental Generalists

A major research emphasis in Japan compared the natural history and ecology of all four species (summarized by Sekiguchi 1988). The Limulacea are essentially estuarine dwellers. They are fully capable, however, of excursions onto the continental shelf in search of prey and perhaps also to redistribute their populations when they become too dense or their local habitat is threatened. But they do not live or thrive everywhere – their distribution is often interrupted and, even within their ranges, their populations vary in numbers. Yet all species have extensive geographic ranges: *Limulus polyphemus*, ranges from 21° N to 44° N and 68° W to 90° W (Fig. 5). *Tachypleus tridentatus* ranges from 12° N to 31° N and 90° E to 125° E, *Carcinoscorpius rotundicauda* from 91° E to 118° E, and 6° S to 20° N, and *T. gigas* from 91° E to 117° E and 6° S to 20° N (Fig. 6). Despite the frequent overlapping of their distributions and habitats, the ecological niches of the three Indo-Pacific species are not directly competitive (Sekiguchi 1988). The extant species exhibit discrete populations – morphometrically and genetically. They probably also exist in physiological races (Shuster 1955, 1979). Due to these characteristics and their ability to cope with wide-ranging environmental conditions, especially salinity and temperature (Towle and Henry