Limits on the Global Distribution of Horseshoe Crabs (Limulacea): Lessons Learned from Two Lifetimes of Observations: Asia and America

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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)

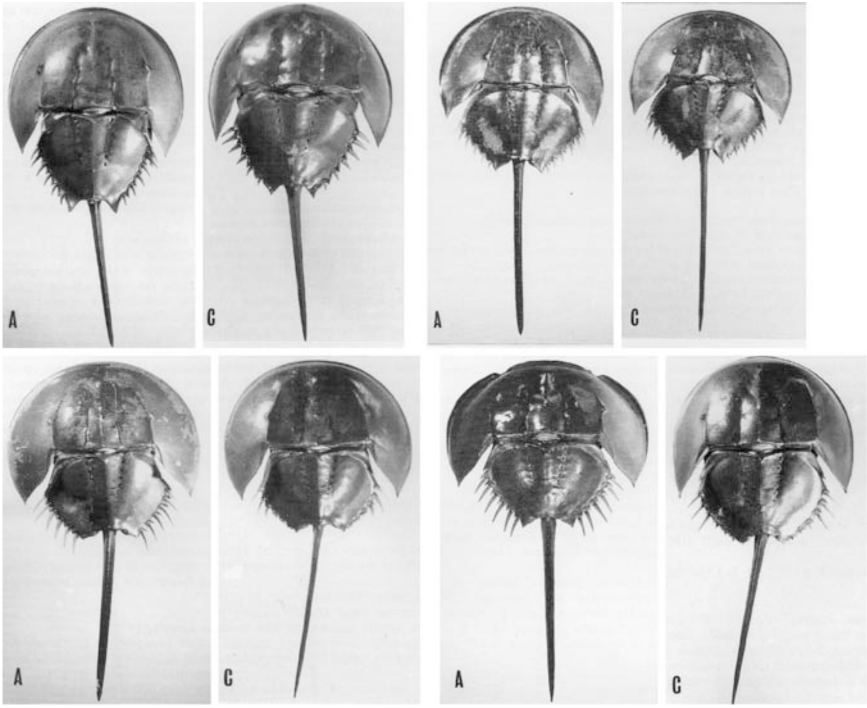

Fig. 1 Dorsal aspects of the adults of the four extant species (A = males; C = females): *Top row* (*left* to *right*): *Limulus polyphemus* and *Carcinoscorpius rotundicauda*; *Bottom row* (*left* to *right*): *Tachypleus gigas* and *Tachypleus tridentatus* (Yamasaki 1988)

Family Tachypleinae
  Tachypleus tridentatus (Leach 1819)
  Tachypleus gigas (Muller 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

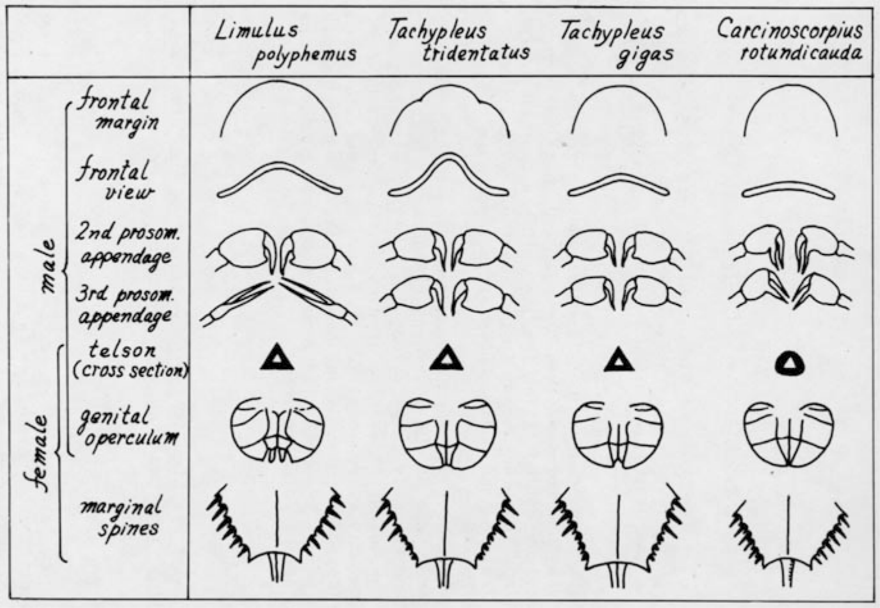

Fig. 2 Distinguishing morphological characteristics of the four species of extant horseshoe crabs (Sekiguchi and Nakamura 1979)

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).

Fig. 3 A comparison of the opisthosomas of *Limulus coffini* (*left*) and *Limulus polyphemus* (*right*) (mold of the fossil, *L. coffini*, courtesy of Dr. J. B. Reeside)

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

Fig. 4 An internal mold of *Mesolimulus walchi* from the private collection of H. Leich, Germany. It is an excellent example of a positive-negative impression; prosomal width = 5.5 cm (Shuster and Anderson 2003)

2003), horseshoe crabs qualify as environmental generalists (Loveland et al. 1997, Eldredge 1991).

Because they are ecological generalists and because their distribution and activities are often described to general terms, we cannot over emphasize the fact that the details in many studies are essentially only accurate for the place, time, and environmental conditions that existed at the time of the study. We tend to generalize, but at the same time we are mindful that horseshoe crabs do not always do what they are expected to do – hence their behavior may fall outside a generality under certain circumstances.

2.4 Significance of the Discreteness of Populations

When morphometric data (Fig. 7) on nearby and on widely separated populations of *Limulus polyphemus* were obtained it led to the deduction that there were discrete populations (Shuster 1955, 1979). The discovery that morphometric

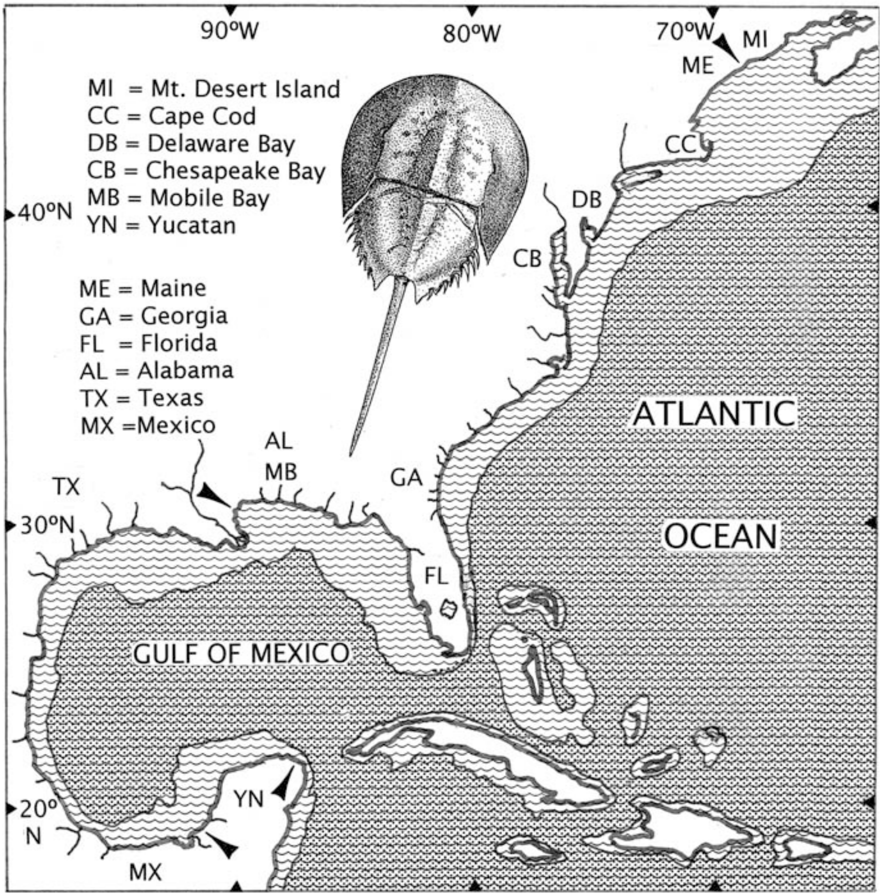

Fig. 5 Breeding populations of the American horseshoe crab, *Limulus polyphemus*, are distributed, intermittently, on the shore of Yucatan and from the Mississippi delta eastward to the Florida Keys and then along the Atlantic coast, Florida to Maine (from about 21°N to 44°N), with occasional strays reported in Texas and Canadian waters. Except for a narrow continental shelf along the southeast coast of Florida, the shelf is broad elsewhere

discrete populations of *L. polyphemus* displayed a latitudinal gradient of smaller-sized adults from Georgia southward and northward from Cape Cod was confirmed by Riska (1981). Similar data (Fig. 8) are available for the three Indo-Pacific species (Yamasaki 1988).

Temperature tolerance (Mayer 1914) and morphometric discreteness led Shuster (1955, 1979) to deduce that these were physiological races (Shuster 1955, 1979). Mayer had reported differences in temperature tolerance of crabs from two populations of *Limulus*. Crabs from Marquesas Keys, Florida, could not withstand the colder temperatures in which crabs from Woods Hole, Massachusetts lived, and, conversely, the northern crabs could not survive in

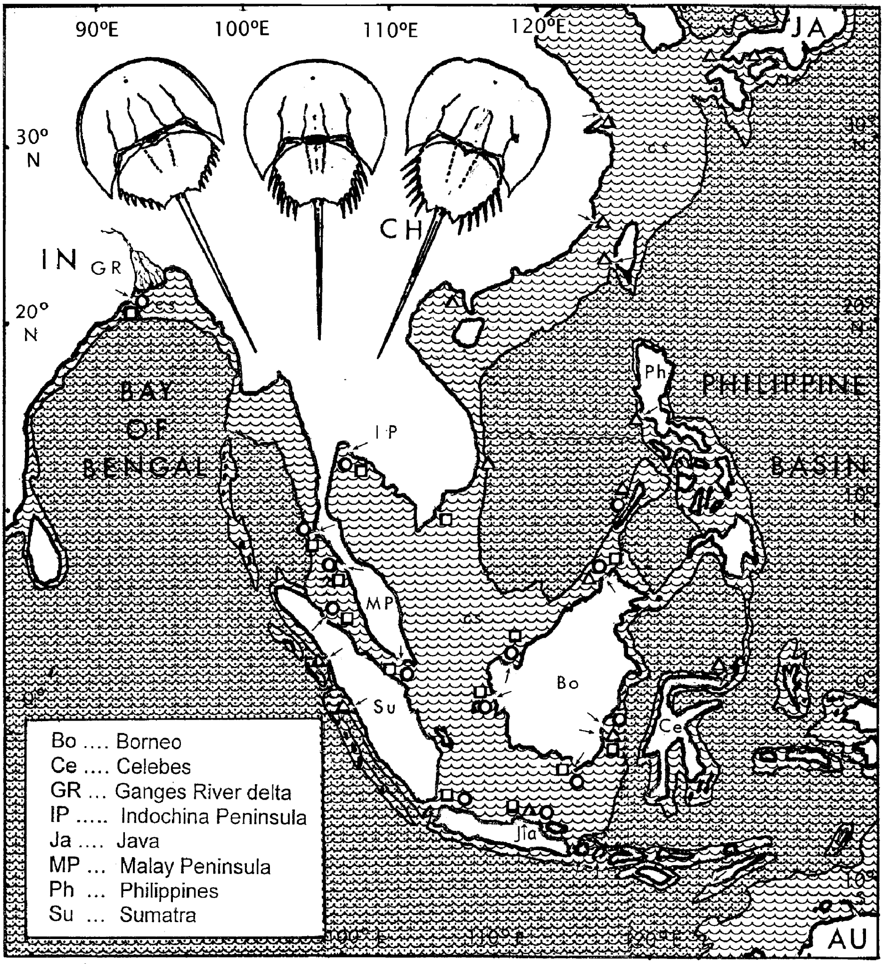

Fig. 6 The continental shelf (cs) is the avenue of distribution for horseshoe crabs. The three Indo-Pacific species are widely distributed with their ranges overlapping in many locations (modified from Anderson and Shuster in Shuster, Barlow and Brockmann 2003, based on Sekiguchi 1988). One or more species were found near most research sites (*small arrows*); *triangles* = *Tachypleus tridentatus* (dorsal view to right in masthead); *squares* = *Tachypleus gigas* (middle of masthead), and *circles* = *Carcinoscorpius rotundicauda* (*left* in masthead); JA = Japan CH = China, IN = India, and AU = Australia

the warmer southern water temperatures. Maximum activity in the Florida crabs occurred at 41°C and at 38°C for the northern crabs. Reynolds and Casterlin (1979) described a range of thermoregulatory behavior in juvenile *Limulus* (prosomal widths from 20 to 50 mm) from the northeastern coast of Gulf of Mexico. They demonstrated that locomotor activity was likely to be optimum in the range of 25°–30°C; temperature, in one way or another, is a major factor in adult size and in activity.

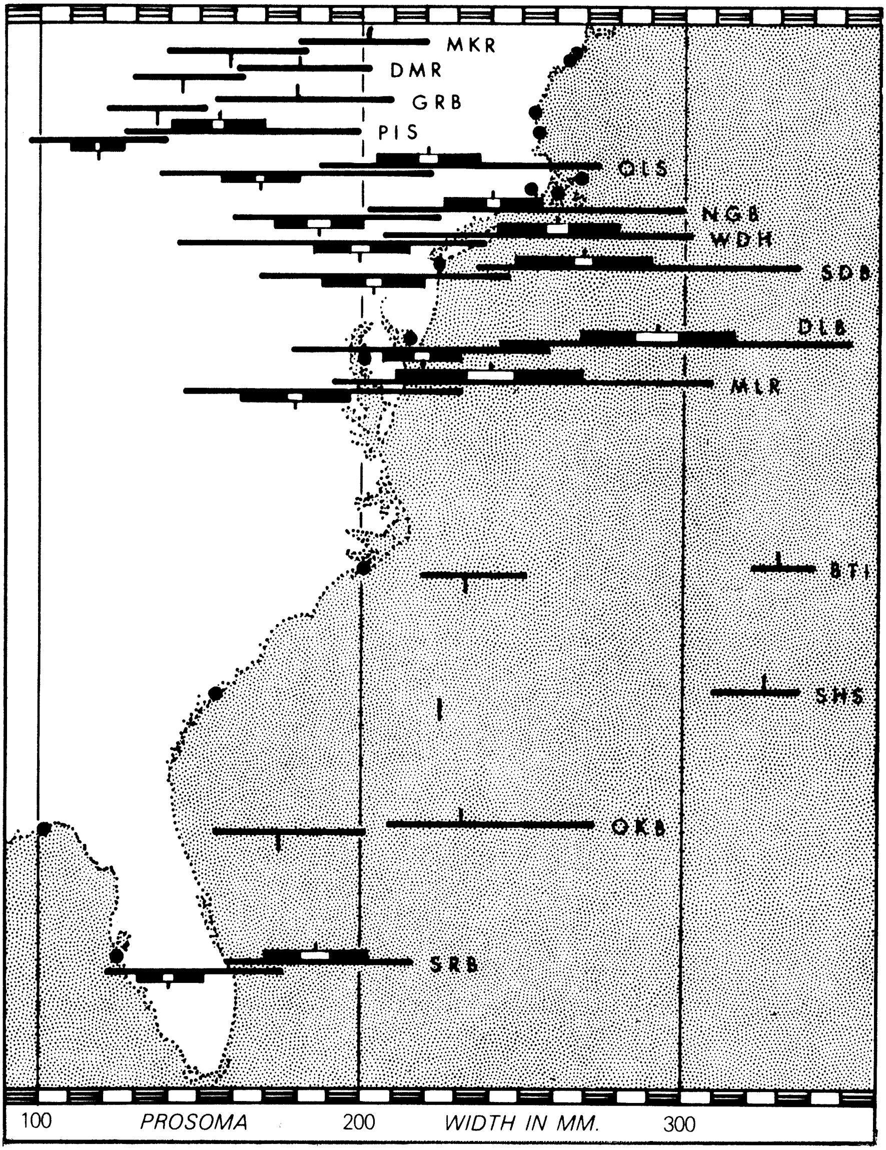

Fig. 7 Populations of *Limulus polyphemus* are morphometrically discrete (Shuster 1955, 1979). Graphic representation of the prosomal widths of adults in millimeters (after technique of Hubbs and Hubbs 1953): range in prosomal width (*horizontal line*); mean (*vertical spike*), one standard deviation (*wide bar*); two standard errors of the mean (*white portion of each bar*); the female dimensions are greater than those of the males. SRB = Sarasota Bay, Florida (27°30′ N); OKB = Ochlockonee Bay, FL; SHS = St. Helena Sound, South Carolina; BTI = Beaufort Inlet, North Carolina; MLR = Miles River, Chesapeake Bay, Maryland; DLB = Delaware Bay, New Jersey; SDB = Sandy Hook Bay, NJ; WDH = Woods Hole, Massachusetts; NGB = Narragansett Bay, Rhode Island; OLS = Pleasant Bay, Cape Cod, MA; PIS = Plum Island Sound, MA; GRB = Great Bay, New Hampshire; DMR = Damariscotta River, ME; MKR = Medomak River, ME (44° N)

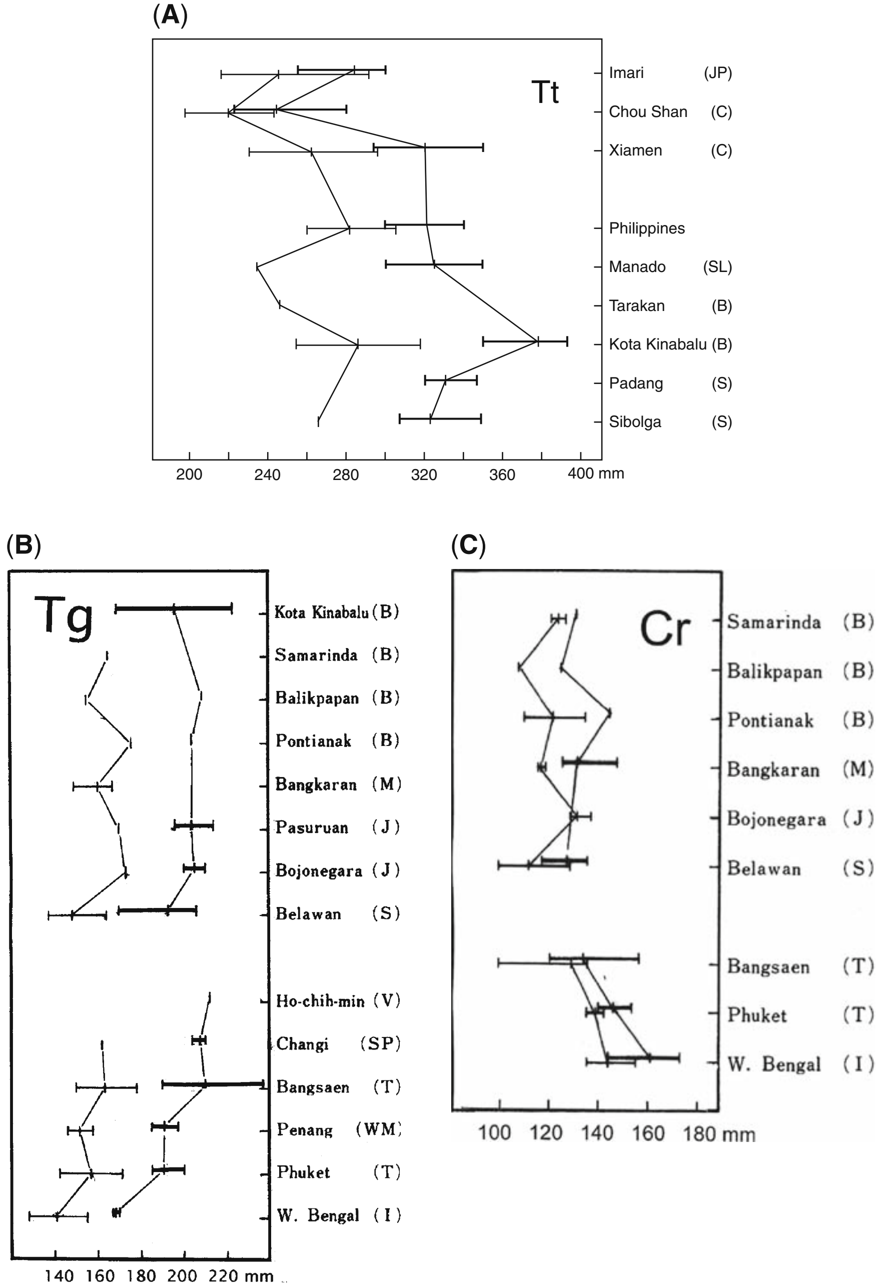

Fig. 8 Populations of the Indo-Pacific species of horseshoe crabs can be defined by their prosomal widths. (**A**) *Tachypleus tridentatus* (Tt). The males (*left-hand* portion of graphs) are smaller than the females; maximum, mean, and minimum widths are shown. Countries are abbreviated as B = Borneo; C = China; JP = Japan; S = Sumatra; SL = Sulawesi (Celebes).

Horseshoe crabs are not gregarious arthropods. Their distribution appears to be closely linked to abundance of the crabs in a population – increasing numbers probably are responsible for increased searches for food. As the crabs get larger, they appear to congregate less and less, especially by sex, except when feeding or breeding. Going their separate ways may be, in part, to escape the possibility of cannibalism by the larger crabs attacking molting crabs.

2.5 Genetic Considerations

Genetic studies substantiate the existence of discrete populations and lend credence to the physiological races concept. Selander et al. (1970) established that electrophoretic variations between four populations of *Limulus polyphemus* were comparable to those of other animals and concluded that the stabilization of their external morphology for at least 200 million years was due to the temporal uniformity of the organic environment and/or genetic homeostasis. Sokoloff (1978) studied eye color and concluded that there were physiological races of *Limulus*. Microsatellite DNA analyses of several *Limulus* populations, from the Gulf of Mexico to New England (Saunders et al. 1986), revealed distinct populations. Pierce et al. (2000) showed that the smaller-sized *Limulus* from the upper Chesapeake Bay were also genetically different from the larger-sized Delaware Bay horseshoe crabs. The latest evidence for genetic differentiation in *Limulus* was provided by a large-scale study of populations throughout their range (King et al. 2003). The extent of the available genetic information leaves little doubt as to the physiological differences of the populations.

Other evidences of relationships between the extant species were demonstrated in a series of developmental and biochemical studies by Sekiguchi and colleagues (1988). Experimental hybridization using reciprocal fertilization of gametes produced viable, swimming larvae only in crosses between *Tachypleus tridentatus* and *Carcinoscorpius rotundicauda*; reciprocal crosses between the three Indo-Pacific species and *Limulus* were non-fertile (Sugita et al. 1988). The diploid number of chromosomes is 26 (*T. tridentatus*), 28 (*T. gigas*), 32 (*C. rotundicauda*), and 52 (*L. polyphemus*) (Iwasaki et al. 1988). Extensive biochemical and immunological studies on the hemocyanin also yielded specific relationships among the species (Sugita et al. 1988). Serological correspondence studies yielded immunological distances that placed the separation of the Indo-Pacific species and *Limulus* at some 130 million years ago while *T. gigas* separated from the other two about 20mya and *T. tridentatus* and *C. rotundicauda* about 10 mya (Shishikura et al. 1982).

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Fig. 8 (continued) (**B**) *T. gigas* (Tg), (**C**) *Carcinoscorpius rotundicauda* (Cr). Countries and cities are abbreviated as B = Borneo; I = India; J = Java; M = Madura; S = Sumatra; SP = Singapore; T = Thailand; V = Vietnam; and WM = West Malaysia. “Samarinda” = a coastal site near Samarinda. Modified from Yamasaki et al. (1988)

2.6 Physiological Considerations

The physiological bases for coping with widely ranging environmental conditions were summarized by Towle and Henry (2003). *Limulus* behaves as an osmotic conformer in salinities above 23 ppt and an osmotic regulator in lower salinities. Horseshoe crabs cope with limited oxygen supplies and, particularly during the spawning season respond to a wide range of temperatures. These studies were pioneered by Charlotte Mangum at the College of William and Mary. Although the physiological responses of different populations to the environmental variables were not compared, it can be assumed that differences exist, at least for temperature tolerance (Mayer 1914).

On the basis of the physiological information, we conclude that the conservative retention of an ancient external morphology masks an up-to-date physiology. Because discrete populations have their own set of environmental tolerances – probably due the wide geographical ranges of the species – the separate populations must be the unit of consideration, rather than the species as a whole, when considering conservation measures. Another overall interpretation of this information is that each major population of *Limulus*, and presumably those of the three Indo-Pacific species, has its own distinct range of environmental adaptability that is less than that for the species as a whole.

3 The Large-Scale Limitations on Distribution

There are at least four large-scale, global, environmental parameters that, spatially and temporally, set limits on the distribution of horseshoe crabs. Of these, continental geomorphology and temperature regimes are two major constraints on the widespread distribution of horseshoe crabs. Basically, the continental shelves define the areas available to horseshoe crabs while low temperatures limit their northernmost occurrence. Tidal types and benthic currents also play a role in the distribution of horseshoe crabs.

3.1 Geology Sets Boundaries

The geologic record strongly suggests that horseshoe crabs have always been shallow water creatures. Doubtless the habitats that we associate with the Limulacea – estuaries, shallow seas, and continental shelves – have always existed some where throughout geologic time, changing only in distribution, quantities, and qualities. But there were always some shallow water habitats where horseshoe crabs could exist, even when the low-salinity region of estuaries and continental shelves comprised the geologic boundaries.

3.2 Estuaries

In recent geologic history estuaries are the breeding and nursery grounds for horseshoe crabs. Perhaps shallow water, intertidal areas have always been their habitats. It seems as if horseshoe crabs evolved adaptations to the relative low-energy levels and the salinity ranges and certain beach conditions. However, we surmise that breeding sites and conditions may not have always been as they are today.

Coastal embayments provide low-energy areas critical in the development of the eggs into larvae. At first glance it may seem that these calmer waters are most important because less stranding would occur during the spawning activity than might occur in rougher waters. But, this is a minor situation. The real reason is that horseshoe crabs cannot spawn in rough surf. Indeed, when waves striking a beach are higher than one foot all or most *Limulus* spawners are swept off the beach (Shuster 1955, 1958).

Populations of *Limulus* exist in wide ranges of salinities with limiting salinities as low as 8–9 parts per thousand, as in the upper Chesapeake Bay, and their eggs can develop in full-strength seawater and hypersaline conditions (Jegla and Costlow 1982, Ehlinger et al. 2003, Ehlinger and Tankersley 2005). Those beaches with an appropriate sediment size, moisture and oxygen content, and warmth are ideal incubators of horseshoe crab eggs (Brady and Schrading 1983). But when did horseshoe crabs begin to use the beaches? It is tempting to surmise that beach egg-laying was less likely until the opisthosomal segments fused and a deep vault was formed during the Devonian some 380 million or so years ago. This created a chamber in which the book gills could retain moisture for a few hours. However, small-sized species such as *Paleolimulus* and *Euproops* probably laid their eggs in superficial surface materials such as matted plant debris. Probably it was not until the larger-sized crabs evolved that beaches came into their own as incubators.

3.3 Continental Shelves

The advent of extensive exploration of the continental shelf by horseshoe crabs must have occurred when they were large-sized, possibly at least as large as 15 cm in prosoma width, and when their populations were so large that they tended to exhaust local concentrations of food resources. Also, if ancient horseshoe crabs were like those of today, they seem to avoid each other except to congregate to spawn or to feed. Thus, shallow water zones, where oceans meet land, became important sources of food. They also served as avenues of distribution, from one estuary to another. Interconnected coastal waterways probably also served as limited avenues of distribution. Given the distance of at least 50 statute miles (57.5 nautical miles) that *Limulus* moves in and about Delaware Bay (Swan 2005), the combination of larger-sized crabs and continental shelves was (are) important in their distribution.

3.4 Latitudinal Limitations

Limulus does not extend south of Yucatan, in comparison with the three Indo-Pacific species that coexist on both sides of the equator (Fig. 6). Why *Limulus* does not exist south of Yucatan may be due to a lack of embayments with suitable spawning and juvenile nursery habitats. Other possible conditions may also create barriers, including the lack of a more southern continental shelf avenue. Although the Indo-Pacific species straddle the equator and fossil horseshoe crabs have been reported from Australia, the extant species no longer exist as far south due to the lack of a continental shelf connection and the fossil species are all that remain in Australia.

All extant species of horseshoe crabs are limited in their northern range, suggesting that the intensity and length of winter temperatures form the northern boundary. Indeed, that kind of temperature regime, in effect, controls the distribution of and the migrations of many marine species. Parr's (1933) graph illustrated the fact that local seasonal temperature regimes are markedly different in the surface water temperature along the Atlantic coast of the United States. Reference to his graph demonstrates that local populations of *Limulus* exist within lesser temperature extremes than the range represented by the species as a whole. Many migrating species of fish cannot negotiate the band of rapidly changing water temperatures that develops during the months of December through March in the vicinity of Cape Hatteras, North Carolina – the drastic change within a few miles creates a thermal barrier. This band weakens as the water warms northward in April and June. A lesser temperature barrier forms during June through October at Cape Cod, Massachusetts. Such seasonal changes in the temperature regimes govern migrations of an important predator of *Limulus,* the juvenile loggerhead turtle (Keinath 2003).

An interpretation of the impacts of the last Great Ice Age upon the four extant species, especially upon *Limulus*, suggests what may happen to the Limulidae during periods of global warming. If the distribution of *Limulus* in the past was limited by low temperatures as it is today, then at the peak of the last ice age some 13,000 years ago *Limulus* may have been no further north than Florida. With rising sea level and water temperatures, *Limulus* may extend its range into Canadian waters.

3.5 Significance of Tidal Type

Our observations suggest that there is a general correlation between the occurrence of spawning sites and the tidal type. For example, populations of *Limulus* exist on the northern shores of Yucatan and along the Florida coast to at least Dauphin Island to the west of the entrance to Mobile Bay, and possibly to the Mississippi delta. However, there are no spawning populations in the western portion of the Gulf of Mexico. Because all other environmental parameters, food, hydroclimate, sandy beaches, etc. are suitable but the tides are not, it has been deduced that the tides, the lack of semi-diurnal tides with sufficient amplitude, are the limiting factor (Shuster 1979). The world-wide distribution of semi-daily, irregular semi-daily, irregular diurnal, and regular diurnal tides delineated by Doty (1957) is a good visual reference. This appears to be true for the Indo-Pacific species. Generally, spawning areas are restricted to those locations where the tides are diurnal (regular and irregular). Yet horseshoe crabs have a wide ability to adapt, a characteristic that may be the reason that they have existed for millennia. Such an adaptation is illustrated by the studies of Ehlinger et al. (2003) and Ehlinger and Tankersley (2003) on how *Limulus* exists in a microtidal, hypersaline lagoon on the east coast of Florida.

3.6 Utilizing Currents

The most rapid mode of horseshoe crab locomotion is scuttling wherein the walking legs, tip-toeing, elevate the ventral surface of a crab slightly off the bottom. Velocity is provided by the flow of water created by the flexing of the operculum and branchiae (book gills) and by benthic currents. Several kinds of observations provide the evidence for their riding the currents, i.e., going with the flow

- in clear shallow waters, especially when emerging from a resting burrow during a flooding tide,
- moving with surge currents (Rudloe and Herrnkind 1976),
- during their approach over intertidal flats to spawning beaches,
- from an experiment with juveniles in a flow tank (Luckenbach and Shuster 1997, Preliminary study on the behavior of juvenile *Limulus* in a flume tank. Unpublished manuscript, cited in Anderson and Shuster 2003), and
- from observations by Oates (2005, Personal communication from benthic video observations on *Limulus* in Delaware Bay) by use of a benthic sled using optical sensors.

4 Conservation Considerations

Because this discussion focuses on global limitations to horseshoe crab distribution, a key question is whether conservation strategies are best implemented on a global or local scale. We suggest that conservation of a species may be, in large part, dependent upon the extent to which local, discrete populations are conserved. In other words, conservation of local, discrete populations adds up to the global conservation of a species. Although diversity within and among species may buffer or otherwise enhance their geologic longevity (Shuster and Anderson 2003), this does not appear to be the major concern of conservationists. The ecological role of horseshoe crabs at Delaware Bay has become famous, scientifically and politically, due to the obligatory diet of migratory shorebirds on horseshoe crab eggs (Botton and Shuster 2003). But this is only one of their roles as a multiple-use resource (Berkson and Shuster 1999). Are all the uses equally important? What are some of the ecological considerations?

4.1 Species Diversity

Apparently there have always been only a few species of horseshoe crabs living at any specific geologic time (Shuster and Anderson 2003). That geologic history suggests that the four extant species are probably about right for the long haul into the future. If so, then all four are candidates for our consideration.

4.2 Physiological Diversity

Horseshoe crabs, as a taxonomic group and for millions of years, have demonstrated a kind of conservation. This is evidenced in their tri-part skeletal anatomy that has existed for millions of years. This has sufficed to enable them to do whatever is physically necessary to survive, except perhaps to back up. Perhaps more importantly, they have combined the conservative anatomical trait with an open-ended physiology. On this, geneticists have provide convincing data based on DNA and other analyses that American horseshoe crabs are still evolving throughout their extensive geographical range – this is plausibly also true for the Japanese, Chinese, and Indian species. Presumably this is in response to local ecological factors. In looking at the data amassed by King et al. (2003), the richness of the genetic picture suggests a reason why horseshoe crabs are physiologically robust: no matter what the environmental trend, there was and probably is a gene pool in at least one population that has or will carry the lineage along to the next geologic epoch.

Horseshoe crabs may have always been associated with tidal waters, particularly in estuarine habitats. They have grown to large sizes in temperature waters suggesting that they extended their ranges either northward from primeval warmer climes or to the south and north from temperate areas. In support of the last point, it is at the extremes of their distribution that they are smaller is size and where the genetic picture suggests that adaptive processes are most pronounced. Thus, examination of horseshoe crabs may reveal more interesting data where they exhibit extremes. This may also apply to comparison of areas where they are few or great in numbers. It might be that studies on the extremes, in range or in numbers, may yield more information than studies on average populations, as in studies of spawning behavior.

Horseshoe crabs have adequate motility to range widely. In a few thousand years they moved from a southern area, possibly in the region of Florida/Georgia, to Maine after the last great ice age (13,000 years ago). Despite their mobility and distribution, however, they have developed discrete populations. This was been demonstrated by morphometric indices (Shuster 1955, 1982, Riska 1981) and confirmed genetically (Saunders et al. 1986, Pierce et al. 2000, King et al. 2005).

4.3 Ecological Role

There is little doubt that horseshoe crabs, due largely to their ultimate large size, longevity, and abundance can be one of the major species in the ecology of coastal areas. They are a source of food for other species, are voracious feeders, and may disturb vast areas of benthic and beach habitats.

4.3.1 As Prey

Several species of birds feed on the eggs and stranded crabs worldwide. But the feeding on the eggs by migratory shorebirds all along the coast of North America, especially the great concentration at Delaware Bay that has attracted the most attention. But the shorebirds are competing with small fish, shrimp, and other benthic dwellers for the eggs (Botton and Shuster 2003). Then there are the predators on horseshoe crabs: fishes (small fish and sharks), the loggerhead turtle; birds (migratory shorebirds on eggs; gulls on eggs and crabs); alligators; pigs and raccoons (deSylva et al. 1962, Shuster 1982, Spraker and Austin 1997). Are any of these groups of feeders more important?

4.3.2 Voracious Predators

Horseshoe crabs are voracious predators on a large number of prey organisms (Botton 1984a, Botton and Shuster 2003). They are certainly competitors with other estuarine organisms (skates, rays, etc.) and with man (soft-shelled clam, razor clam, quahaug, surf clam, blue mussel).

4.3.3 As Excavators

Horseshoe crabs typically burrow, shallowly in the substrate when resting, feeding, or spawning (Shuster 1955, 1982, Botton 1984b, Kraeuter and Fegley 1994). The multitude of tracks and pits left on a beach after a heavy spawning event during calm weather looks like the aftermath of a miniature tanks battle. Whether the disturbance of beach sediments or the benthic excavations are significant factors in erosion or affecting ecological parameters has not been examined.

5 Conclusions

The conservative skeletal anatomy of horseshoe crabs, combined with genetic physiological diversity, has resulted in adept environmental generalists. This has enabled them to adapt to a broad range of environmental conditions and to survive for eons. The morphometric and genetic demonstrations that horseshoe crabs exist in discrete populations strongly indicate that any conservation program must recognize the uniqueness of each population as a potential physiological subspecies. We also need a better understanding of the ecological impact of horseshoe crabs.

Understanding horseshoe crabs and their habitat is a key to horseshoe crab conservation, one reason why sessions in this symposium have been devoted to the biology of horseshoe crabs and to their habitat requirements, management, and restoration. Because horseshoe crabs exist in discrete populations, conservation or management programs plans must consider not only the species but its separate populations and their habitats. Although horseshoe crabs have been primarily residents of estuaries and tidal streams, horseshoe crabs have moved from one estuary to another via continental shelves, especially after the last Great Ice Age.

Perhaps the best way to underpin a worldwide horseshoe crab conservation effort is to analyze as many populations as possible, morphometrically and genetically, and their numbers and extent of habitat. Basically, while the broad picture may be the same, what occurs in one habitat for one population under certain environmental conditions may never be observed exactly again; thus, the value of many observations. One reason why Delaware Bay has been so attractive to us and many others is due to its extraordinary large population of horseshoe crabs. This provides a stark contrast to habitats that support lesser numbers of crabs.

Our discussion has dealt with natural barriers to the distribution of horseshoe crabs. We have not included other environmental parameters due to man-induced stresses on the crabs, such as the multiple commercial uses of the crabs, changes in ecosystems, coastal construction, or pollution. Thus, because man can restrict or eliminate suitable habitat and ecosystems, we may create environmental conditions that horseshoe crabs may not be able to successfully adapt to or avoid. Therefore, future attention to favorable habitat conservation and preservation could be as large or larger problem than just managing horseshoe crab populations.

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