The hippo's tale: how the anatomy and physiology of Late Neogene *Hexaprotodon* shed light on Late Neogene environmental change

Nina G. Jablonski*

Department of Anthropology, California Academy of Sciences, Golden Gate Park, San Francisco CA 94118-4599, USA

Abstract

Modern hippopotamuses are strongly dependent on permanent water because of the structure and properties of their skin, and because they forage on vegetation located close to watercourses. In the fossil record of Asia, the disappearance of hippopotamids (best represented by *Hexaprotodon sivalensis*) during the late Neogene and Pleistocene was due to a dramatic increase in seasonal patterns of rainfall and river flow, which would have resulted in many river systems being dry for months of the year. The lack of permanent water resulted in the disappearance of *He. sivalensis* from Asia. Heightened seasonality of rainfall resulted from an intensification of the winter and summer monsoons during the period between 3.6 and 2.6 Ma. Because of the exquisite sensitivity of hippopotamuses to the availability of permanent water, well-established dates for the last appearance of *He. sivalensis* in Asian fossil sequences can be used as direct indicators of the onset of highly seasonal patterns of rainfall and river flow.
© 2003 Elsevier Ltd and INQUA. All rights reserved.

1. Introduction

Vertebrate paleoantologists are generally consumers, not providers, of paleoenvironmental information. It is common, for instance, for vertebrate paleontologists to refer to analyses of paleosols or pollen profiles for purposes of reconstructing vegetation types in a species' habitat and, in turn, gaining insight into the species' diet or mode of locomotion. Some of the most useful paleoenvironmental information informs vertebrate paleontologists about characteristics of the environment that most directly influence a species' reproductive success, such as ambient temperature, availability of water, or distribution of probable food sources throughout the year. Rarely are characteristics of vertebrate animals used to reconstruct specific features of the environment. In most cases, this is because vertebrates— especially large mammals—are considered coarse indicators of the environment because of their ability to range over large areas and many microenvironments.

There are notable examples, however, of vertebrate paleontological evidence being used to shed light on the nature of paleoenvironments. In most of these cases, fossil species that are closely related to modern species with known and specific habitat and dietary preferences are used to indicate the nature of past vegetation communities. Excellent examples of this come from the work of John Rensberger on hypsodonty in rodents and horses and the expansion of grasslands during the late Tertiary of North America (Rensberger, 1982, 1984) and that of Elisabeth Vrba on the environmental significance of the appearance and prevalence of tribes of Plio-Pleistocene African antelopes (Vrba, 1974). Reed (1998) has also shown that the composition of large mammal communities can shed light on ancient environments. Specifically, particular types of vegetation support predictable percentages of large mammals (e.g., arboreal, grazing, etc.). These adaptations can be used to predict paleovegetation and to portray the community structure of fossil assemblages.

This study differs from previous studies in that it is not focused on the reconstruction of paleoenvironments through analysis of the composition of fossil mammal communities or assemblages, or of the actual preserved anatomy of particular fossil species. Rather, it draws upon the records of first and last appearance of a particular species, phylogenetic inference, and parsimony in order to shed light on the timing of an important series of events during the late Tertiary paleoenvironmental history of south Asian. Specifically, this study draws upon the spatio-temporal distribution of the extinct hippopotamus, *Hexaprotodon sivalensis*, and the inferred properties of its skin to reconstruct

*Tel.: +1-415-750-7161; fax: +1-415-750-7346.
E-mail address: njablonski@calacademy.org (N.G. Jablonski).

probable changes in the seasonal flow of rivers (and the development of collateral riverine vegetation) in south Asia as a result of the intensification of the Asian monsoon during the Late Miocene.

2. Why hippos? Use of the hippopotamus as a tool in paleoenvironmental reconstruction

Hippopotamuses are represented today only by two monotypic genera, *Hippopotamus* and *Hexaprotodon*, and are restricted to Africa. The larger and more widely distributed hippopotamus species of sub-Saharan Africa is *Hi. amphibius*, the common hippo. The smaller and less common species is *He. liberiensis*, the pygmy hippo, known today only from the countries of Guinea Bissau, Guinea, Liberia, and Ivory Coast (Eltringham, 1999). A tiny, isolated and possibly extinct population is also known from Nigeria (Kingdon, 1989).

Modern hippos are unique among terrestrial mammals in their total dependence on permanent water for living sites. The distribution of both species in Africa closely follows the courses of rivers and lake margins (Kingdon, 1979; Eltringham, 1993a, b). The common hippo inhabits rivers within open country, spending its day in the water, but emerges at night to graze and forage on land, often several kilometers from water (Mackie, 1976; Eltringham, 1993a). In rivers such as the Limpopo, bordering South Africa and Zimbabwe, common hippos occupy the larger permanent pools, moving up and down river during flood season and returning to these pools as flood waters subside (Smithers, 1971). Calves are born during high rainfall (flooding) months (Laws and Clough, 1965; Eltringham, 1999), when vegetation along river banks is lush and plentiful and permits females to forage ad libitum, close to the safety of the river. Generally, common hippos are more abundant in wide and slow-moving rivers than in rapids and rocky patches (Attwell, 1963). They prefer areas of slack and relatively shallow water, with gently shelving beaches where animals can lie half-immersed and sleep, and the young can suckle without swimming (Olivier and Laurie, 1974). Common hippos are known to migrate long distances within river systems and, occasionally over land, during the dry season in order to reach water courses of sufficient depth (Sidney, 1965; Viljoen, 1980). The animals suffer badly during droughts, with high mortality attributed to the combined effects of drying of rivers and pools, and the lack of nearby food (Sidney, 1965).

The habits of the pygmy hippo have been less well studied than those of the common hippo, but is known to be confined to forested regions, where it spends its days hidden in swamps, wallows, rivers, or in hollows under the banks of streams (Eltringham, 1993b). Pygmy hippos emerge at night, treading well-defined forest trails to forage for leaves, roots, and fallen fruits within the forest, often more than a kilometer away from their home stream (Kingdon, 1989; Eltringham, 1993b). For both *Hi. amphibius* and *He. liberiensis*, open water is not essential because the animals can survive in muddy wallows. They must, however, have access to permanent water, where they can return during the dry season (Eltringham, 1999).

Hippos are dependent on permanent water primarily because their skin must remain moist lest it crack if exposed for long periods (Luck and Wright, 1964). In both *Hi. amphibius* and *He. liberiensis*, the most superficial layer of the skin, the stratum corneum, is thin, smooth and dense, and permits a higher rate of transepidermal water loss than has been observed for any other mammal (Luck and Wright, 1964; Olivier, 1975). This water loss occurs directly through the skin, not as a result of sweating. Hippos, in fact, lack sweat glands (Olivier, 1975). Olivier (1975) speculated that a very high rate of water loss across the skin, unrelated to glandular activity, requires hippos to adopt a predominantly aquatic life. This is borne out by a subsequent physiological study showing that a high rate of transepidermal water loss facilitates evaporative cooling, which is necessary to counter the animal's heat load (due to convection and metabolism) (Wright, 1987). Although we cannot determine whether it was the aquatic habitus or the properties of the skin that evolved first, application of the principle of parsimony dictates that the common ancestor of modern hippos must have shared in the possession of skin that permitted a high rate of transepidermal water loss (Fig. 1). This shared characteristic has tied both the common (*Hippopotamus*) and pygmy hippo (*Hexaprotodon*) lineages to sources of
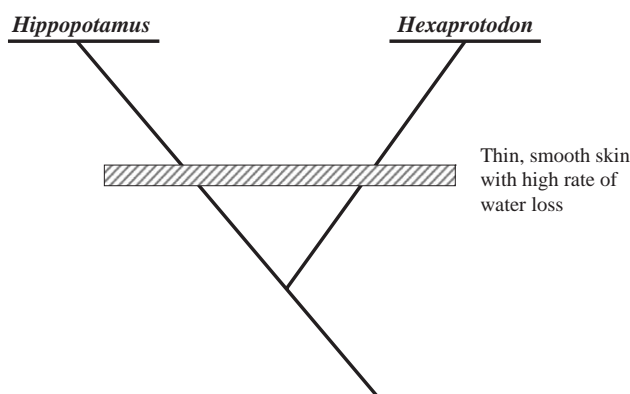

Fig. 1. The presence of thin, smooth skin with a high rate of water loss is a shared derived characteristic (synapomorphy) of the clade of modern hippopotamuses, which comprises the common hippo, *Hi. amphibius*, and the pygmy hippo, *He. liberiensis*. The date of the lineage splitting cannot be determined accurately from the fossil record, but was probably a late Miocene event.

permanent water. The unique anatomy and physiology of hippo skin thus becomes the key to understanding why hippos are potentially very good paleoenvironmental indicators.

It also should be noted that hippos are tied to permanent sources of freshwater because of their feeding habits. Hippos generally remain close (1–3 km) to their home watercourse during their nocturnal foraging expeditions (Smithers, 1971; Mackie, 1976; Eltringham, 1999), although nocturnal excursions as long as 6–10 km have been reported for the common hippo (Lock, 1972; Laws et al., 1975). The distance traversed during nocturnal foraging varies by season, with shorter distances traveled during the rainy season when vegetation on river banks is more abundant (Laws et al., 1975). Limits to the length of foraging trips are influenced by thermoregulatory considerations as well as by availability of food. The endogenous heat generated by locomotion could not be dissipated unless the animal maintained a moist integument (Wright, 1987).

The modern common hippo is generally considered to be a grazer, although it does include some browse in its diet (Kingdon, 1979); it is completely dependent for its sustenance on grasses or other vegetation growing near permanent rivers or streams. The density of *Hi. amphibius* populations is strongly related to the grazing potential of river margin areas (Viljoen and Biggs, 1998), a fact that can be related back to the requirements of female hippos and their calves for high-quality graze located close to a watercourse. The modern pygmy hippo is a more eclectic browser, but is still dependent on vegetation found close to its home stream (Kingdon, 1989; Eltringham, 1993b). It is significant that stable isotope analysis of the dental enamel of early Pliocene *He. harvardi* from the Nawata Formation of the Lothagam sequence of western Kenya shows that, like the modern *Hippopotamus*, *He. harvardi* was predominantly a grazer (Cerling et al., 2001).

3. The evolutionary history and fossil record of hippos

The evolutionary relationships and biogeographical history of the hippos are reasonably well understood thanks to their distinctive craniodental anatomy and their common preservation in Tertiary and Quaternary fossil deposits of the Old World. The origins of the Hippopotamidae are not clear, but molecular evidence has demonstrated that, among living mammals, hippos are most closely related to whales and form a sister group with them (Ursing and Arnason, 1998). The ancestors of the Hippopotamidae (probably members of the Family Anthracotheriidae) and extant whales are estimated to have last shared a common ancestor about

54 Ma ago (Ursing and Arnason, 1998). True hippopotamid fossils are first detected in the early Miocene Kulu Warega deposits of Rusinga Island, Kenya (Coryndon, 1978), and the family is considered to have had a center of evolution during the late Neogene of Africa (Kahlke, 1990).

On morphological grounds, the Asian hippopotamids appear to be more closely related to the modern pygmy hippo than to the common hippo and thus carry the genus name *Hexaprotodon*. The date of the splitting of *Hexaprotodon* into African and Asian lineages cannot be determined exactly from fossil and geochronological evidence, but appears to have been a late Miocene event. In Africa, the earliest occurrence of a well-defined hexaprotodont hippo is at Lothagam in western Kenya at about 6 Ma (Coryndon, 1978). The earliest well-documented occurrences of *Hexaprotodon* in Asia are from Nepal and Pakistan, where they appear to be contemporaneous with the African finds (Corvinus and Rimal, 2001; Barry et al., 2002). A firmly dated first appearance of *He. sivalensis* in the Siwalik sequence of northern Pakistan is dated at 5.9 Ma, with an inferred first appearance as early as 6.1 Ma (Barry et al., 2002). *He. sivalensis* has also been recognized in fossil beds from the Siwalik Hills of northern India, and from a variety of poorly dated late Neogene and early Pleistocene sites in central India (Narmada River), central and southern Myanmar (the Irrawaddy Formation), southwestern China (Yunnan Province), Sri Lanka, western Thailand, Malaysia, and Java (Kahlke, 1990).

The last appearance of *He. sivalensis* in the Pakistani Siwaliks is firmly dated at 3.5 Ma, but the species may have persisted until 2.2 Ma (Barry et al., 2002). In Nepal, the last appearance of *He. sivalensis* in Siwalik deposits is not yet accurately documented, but the taxon may have persisted longer than in Pakistan; the species is also known from the Plio-Pleistocene deposits of the Kathmandu Valley (Jablonski et al., in preparation-a, b). In the well-dated Pliocene sequence of the Samwal and Kakra Formations of the Mangla-Samwal Anticline Range of Pakistan, *He. sivalensis* is a common element of the fauna older than 2.56 Ma, but is scarce in beds younger than 2.40 Ma (Hussain et al., 1992). Its disappearance from the late Pliocene upper Samwal Formation has been interpreted as due to the change from large-scale to small-scale streams, and the disappearance of permanent fresh water (Hussain et al., 1992). The last glacial period of the Pleistocene witnessed the disappearance of all the hippos from Asia, with last interglacial populations in central India (Jabalapur City, Madhya Pradesh State), western India (Maharashtra State), Java (Ngandong fauna), and the Kathmandu Valley of Nepal having been the last to go (Kahlke, 1990; Jablonski et al., in preparation-a).

4. The hippo's tale: seasonality of rainfall and watercourse volume predicted from fossil occurrences of Hexaprotodon

The Late Neogene witnessed major global climatic changes, which can be attributed in part to the uplift of the Tibetan (Qinghai-Xizang) Plateau. In Asia (Ruddiman and Kutzbach, 1989; Partridge et al., 1995; An et al., 2001), these include climatic cooling and increased seasonality of rainfall as a result of the onset of the Indian and east Asian monsoons. Copious geological and biotic evidence, most recently summarized for the Siwalik sequence of the Potwar Plateau of Pakistan by Barry and colleagues (Barry et al., 2002), documents the concatenated environmental and faunal ramifications of these changes. To briefly summarize, significant changes in patterns of precipitation are detected beginning 9.2 Ma, with a shift to a drier and more seasonal climate. After 8.1 Ma, significant amounts of C_4 grasses began to appear, and by 6.8 Ma, floodplain habitats rich in C_4 grasses are common (Barry et al., 2002). Very similar trends are observed in China (An et al., 2001). Thus, the hippopotamus *He. sivalensis* first appears in the fossil record of Asia as a migrant from Africa at a time when the sub-Himalaya was covered by large braided river systems, with extensive, flanking, grassy floodplains. These river systems, especially the smaller channels, witnessed seasonal patterns of flow (Barry et al., 2002), but do not appear to have undergone wide-scale seasonal desiccation.

Simultaneous intensification of both the summer and winter monsoons in Asia, resulting in an amplification of seasonality, is observed in the paleoenvironmental records of the Loess Plateau of China between 3.6 and 2.6 Ma (An et al., 2001). These events appear to be related to additional, incremental uplift or extension of the Tibetan Plateau (An et al., 2001). This period of enhanced uplift is accompanied by a pronounced increase in sediment flux from the main river systems draining the Himalayas and Tibetan Plateau (An et al., 2001), indicating an intensification of monsoonal rainfall on freshly exposed sedimentary rock surfaces (Partridge et al., 1995).

The Asian monsoon is one of the major components of the global climate system and its evolution has played a significant role in our understanding of global climates (Webster, 1987, 1994; Hastenrath, 1991; Hastenrath and Greischar, 1993; Webster et al., 1998). The Asian summer and winter monsoons dominate the seasonal winds, precipitation and runoff patterns, and the character of land vegetation over southern and eastern Asia. The winter monsoon is characterized by high pressure over northern Asia (the Siberian high), northeast winds across the South China Sea (which intensify during cold surges), and enhanced precipitation in the Austral-Asian equatorial zone. In most of the Northern

Hemisphere, the winter monsoon is considered to be a cold, dry period. The summer monsoon circulation is characterized by low pressure over Tibet, strong south-westerly winds, upwelling in the Arabian Sea, and high precipitation over southern and eastern Asia. When lay people refer to "the monsoon" or "monsoon rains", it is the summer monsoon to which they are generally referring.

Paleobiologists interested in environmental changes of the late Neogene in Asia often ponder the question of when highly seasonal patterns of rainfall and river flow became established in the main river systems of the sub-Himalaya. The complete dependence of hippos on permanent water sources and the probable preference of these animals for large, slow-moving rivers provide a long-awaited piece of evidence in this connection. Because of the water-dependent properties of their skin and the limits on the length of their foraging trips (related to their skin and problems of thermoregulation during exercise), hippos would have been among the first mammals to suffer local and, finally, continental extinction as a result of highly intensified seasonality of rainfall and river flow. Although modern *Hi. amphibius* is able to migrate through river systems or for short distances overland at times of drought to reach suitable water courses, it is likely that wide-scale, months-long drought would have been devastating to ancient hippopotamus populations. The close correspondence in timing between the latest Neogene intensification of the Asian monsoons (3.6–2.6) (An et al., 2001) and the dramatic reduction in prevalence of hippopotamids from Pakistani sites on the Potwar Plateau 3.5 Ma (Barry et al., 2002) and the Samwal Formation between 2.56 and 2.40 Ma (Hussain et al., 1992) suggests a cause and effect relationship between the two events. It is therefore suggested here that the disappearance of hippopotamuses from the fossil record of Asia in the Plio-Pleistocene is directly related to dramatic changes in seasonal patterns of river flow, resulting from intensification of the summer and winter monsoons. As ages for the last confirmed appearances of *He. sivalensis* in the fossil record become better established for different sedimentary sequences in Asia, a clearer picture of late Neogene and Pleistocene habitats for those regions will emerge.

References

An, Z.-S., Kutzbach, J.E., Prell, W.L., Porter, S.C., 2001. Evolution of Asian monsoons and phased uplift of the Himalaya-Tibetan plateau since Late Miocene times. Nature 411, 62–66.

Attwell, R.I.G., 1963. Surveying Luangwa hippo. The Puku 1, 29–50.

Barry, J.C., Morgan, M.E., Flynn, L.J., Pilbeam, D., Behrensmeyer, A.K., Raza, S.M., Khan, I.A., Badgley, C., Hicks, J., Kelley, J., 2002. Faunal and environmental change in the Late Miocene Siwaliks of Northern Pakistan. In: Paleobiology Memoirs, Memoir 3. The Paleontological Society, Lawrence, KS, 71pp.

Cerling, T.E., Harris, J.M., Leakey, M.G., 2001. Isotope paleoecology of the Nawata and Nachukui formations at Lothagam, Turkana Basin, Kenya. In: Leakey, M.G., Harris, J.M. (Eds.), Lothagam: The Dawn of Humanity in Eastern Africa. Columbia University Press, New York, pp. 577–598.

Corvinus, G., Rimal, L.N., 2001. Biostratigraphy and geology of the Neogene Siwalik Group of the Surai Khola and Rato Khola areas in Nepal. Palaeogeography, Palaeoclimatology, Palaeoecology 165, 251–279.

Coryndon, S.C., 1978. Hippopotamidae. In: Maglio, V.J. (Ed.), Evolution of East African Mammals. Harvard University Press, Cambridge, MA, pp. 483–495.

Eltringham, S.K., 1993a. The common hippopotamus (*Hippopotamus amphibius*). In: Oliver, W. (Ed.), Pigs, Peccaries and Hippos. IUCN, Gland, pp. 43–55.

Eltringham, S.K., 1993b. The pygmy hippopotamus (*Hexaprotodon liberiensis*). In: Oliver, W. (Ed.), Pigs, Peccaries and Hippos. IUCN, Gland, pp. 55–60.

Eltringham, S.K., 1999. The Hippos. Academic Press, Cambridge, 184pp.

Hastenrath, S., 1991. Climate Dynamics of the Tropics. Kluwer Academic Publishers, Boston, 488pp.

Hastenrath, S., Greischar, L., 1993. The monsoonal heat budget of the hydrosphere atmosphere system in the Indian Ocean sector. Journal of Geophysical Research 98, 6869–6881.

Hussain, S.T., van den Bergh, G., Steensma, D.K.J., de Visser, J.A., de Vos, J., Arif, M., van Dam, J., Sondaar, P.Y., Malik, B., 1992. Biostratigraphy of the Plio-Pleistocene continental sediment (Upper Siwaliks) of the Mangla-Samwal Anticline, Azad Kashmir, Pakistan. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen 95, 65–80.

Jablonski, N.G., Chaplin, G., Corvinus, G., in preparation-a. A review of the vertebrate fossil fauna of the Kathmandu Valley, central Nepal, with a report of newly discovered fossils. Proceedings of the California Academy of Sciences.

Jablonski, N.G., Corvinus, G., Chaplin, G., Rimal, L.N., in preparation-b. A review of the vertebrate fossil fauna of the Siwalik sequence of Western Nepal, with a description of new fossil finds. Proceedings of the California Academy of Sciences.

Kahlke, V.R.-D., 1990. Zum Stand der Erforschung fossiler Hippopotamiden (Mammalia, Artiodactyla) Eine Ubersicht. Quartarpalaontologie 8, 107–118.

Kingdon, J., 1979. East African Mammals, Vol. I. University of Chicago Press, Chicago, 446pp.

Kingdon, J., 1989. Island Africa. Princeton University Press, Princeton, 287pp.

Laws, R.M., Clough, G., 1965. Observations on reproduction in the hippopotamus, Hippopotamus amphibius. Journal of Reproduction and Fertility 9, 369–370.

Laws, R.M., Parker, I.S.C., Johnstone, R.C.B., 1975. Elephants and their Habitats. Clarendon Press, Oxford, 376pp.

Lock, J.M., 1972. The effects of hippopotamus grazing on grasslands. The Journal of Ecology 60, 445–467.

Luck, C.P., Wright, P.G., 1964. Aspects of the anatomy and physiology of the skin of the hippopotamus (*H. amphibius*). Quarterly Journal of Experimental Physiology and Cognate Medical Sciences 49, 1–14.

Mackie, C., 1976. Feeding habits of the hippopotamus on the Lundi River, Rhodesia. Arnoldia Rhodesia 7, 1–16.

Olivier, R.C.D., 1975. Aspects of the skin physiology in the pigmy hippopotamus Choeropsis liberiensis. Journal of Zoology (London) 176, 211–213.

Olivier, R.C.D., Laurie, W.A., 1974. Habitat utilization by hippopotamus in the Mara River. East African Wildlife Journal 12, 249–271.

Partridge, T.C., Bond, G.C., Hartnady, C.J.H., deMenocal, P.B., Ruddiman, W.F., 1995. Climatic effects of late Neogene tectonism and volcanism. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Haven, pp. 8–23.

Reed, K.E., 1998. Using large mammal communities to examine ecological and taxonomic structure and predict vegetation in extant and extinct assemblages. Paleobiology 24, 384–408.

Rensberger, J.M., 1982. Patterns of dental change in two locally persistent successions of fossil aplodontid rodents. In: Kurten, B. (Ed.), Teeth: Form, Function and Evolution. Columbia University Press, New York, pp. 323–349.

Rensberger, J.M., 1984. Functional evolution of the cheek tooth pattern and chewing direction in Tertiary horses. Paleobiology 10, 439–452.

Ruddiman, W.F., Kutzbach, J.E., 1989. Forcing of Late Cenozoic northern hemisphere climate by plateau uplift in southern Asia and the American West. Journal of Geophysical Research 94, 18409–18427.

Sidney, J., 1965. The past and present distribution of some African ungulates. Transactions of the Zoological Society of London 30, 89–130.

Smithers, R.H.N., 1971. The Mammals of Botswana. The Trustees of the National Museums of Rhodesia, Salisbury.

Ursing, B.M., Arnason, U., 1998. Analyses of mitochondrial genomes strongly support a hippopotamus–whale clade. Proceedings of the Royal Society of London B 7, 2251–2255.

Viljoen, P.C., 1980. Distribution and numbers of the hippopotamus in the Olifants and Blyde Rivers. South African Journal of Wildlife Research 10, 129–132.

Viljoen, P.C., Biggs, H.C., 1998. Population trends of hippopotami in the rivers of the Kruger National Park, South Africa. In: Dunstone, N., Gorman, M. (Eds.), Behavior and Ecology of Riparian Mammals, Vol. 71. Cambridge University Press, Cambridge, pp. 251–279.

Vrba, E.S., 1974. Chronological and ecological implications of the fossil Bovidae at the Sterkfontein Australopithecine site. Nature 250, 19–23.

Webster, P.J., 1987. The elementary monsoon. In: Fien, J., Stephens, P. (Eds.), Monsoons. Wiley, New York, pp. 3–32.

Webster, P.J., 1994. The role of hydrological processes in ocean–atmosphere interactions. Review of Geophysics 32, 427–476.

Webster, P.J., Magana, V.O., Palmer, T.N., Shukla, J., Tomas, R.A., Yanai, M., Yasunari, T., 1998. Monsoons: processes, predictability, and the prospects for prediction, in the TOGA decade. Journal of Geophysical Research 103, 14451–14510.

Wright, P.G., 1987. Thermoregulation in the hippopotamus on land. South African Journal of Zoology 22, 237–242.