

Rhinoceros sondaicus (Perissodactyla: Rhinocerotidae)

COLIN P. GROVES AND DAVID M. LESLIE, JR.

School of Archaeology and Anthropology, Building 14, Australian National University, Canberra, Australian Capitol Territory 0200, Australia; colin.groves@anu.edu.au (CPG)

United States Geological Survey, Oklahoma Cooperative Fish and Wildlife Research Unit and Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK 74078-3051, USA; cleslie@usgs.gov (DML)

Abstract: *Rhinoceros sondaicus* Desmarest, 1822, commonly called the Javan rhinoceros or lesser one-horned rhinoceros, is the most critically endangered large mammal on Earth with only 40–50 extant individuals in 2 disjunct and distant populations: most in Ujung Kulon, West Java, and only 2–6 (optimistically) in Cat Loc, Vietnam. *R. sondaicus* is polytypic with 3 recognized subspecies: *R. s. sondaicus* (currently West Java), *R. s. inermis* (formerly Sunderbunds; no doubt extinct), and *R. s. annamiticus* (Vietnam; perhaps now extinct). *R. sondaicus* is a browser and currently occupies lowland semievergreen secondary forests in Java and marginal habitat in Vietnam; it was once more widespread and abundant, likely using a greater variety of habitats. *R. sondaicus* has a very spotty history of husbandry, and no individuals are currently in captivity. Conservation focuses on protection from poaching and habitat loss. Following decades-long discussion of captive breeding and establishment of a 3rd wild population, conservation and governmental agencies appear closer to taking such seriously needed action on the latter.

Key words: Cat Loc, critically endangered, Java, Javan rhinoceros, lesser one-horned rhinoceros, relict species, Ujung Kulon, Vietnam

© 26 September 2011 by the American Society of Mammalogists
Synonymy completed 18 December 2010
DOI: 10.1644/887.1

www.mammalogy.org



Rhinoceros sondaicus Desmarest, 1822 Javan Rhinoceros

rhinoceros sondaicus Desmarest, 1822:399. Type locality “Sumatra;” corrected to “Java” by Desmarest (1822:547).

[*Rhinoceros*] *Javanicus* É. Geoffroy Saint-Hilaire and F. Cuvier, 1824:unnumbered page associated with pl. 309, vol. vi, livr. 45. Type locality “Java.”

R[*hinoceros*]. *Camperis* de Blainville in Griffith, Hamilton-Smith, and Pidgeon, 1827:291. No type locality given.

Rh[*inoceros*]. *Javanus* G. Cuvier, 1829:247. Incorrect subsequent spelling of *Rhinoceros javanicus* É. Geoffroy Saint-Hilaire and F. Cuvier, 1824.

R[*hinoceros*]. *Camperii* Jardine, 1836:181. Incorrect subsequent spelling of *Rhinoceros camperis* de Blainville in Griffith, Hamilton-Smith, and Pidgeon, 1827.

Rhinoceros inermis Lesson, 1838:514. Type locality “Sundries [= Sunderbunds],” West Bengal, India, and Bangladesh.

Rhinoceros sivalensis Falconer and Cautley, 1847:pl. 73, figs. 2 and 3; pl. 74, figs. 5 and 6; pl. 75, figs. 5 and 6. Type locality “upper Siwaliks;” restricted to “Ratnapura series,” Ceylon by Deraniyagala (1938); fossil probably from the Upper Pleistocene.



Fig. 1.—Rare images of an adult male *Rhinoceros sondaicus* from Ujung Kulon, West Java, in 1978; note the diagnostic dermal shields and prehensile upper lip used to grab forage in the bottom image. Photographs by H. Ammann, used with permission.

Rhinoceros nasalis Gray, 1868:1012. Type locality “Borneo.”
Rhinoceros floweri Gray, 1868:1015. Type locality “Sumatra.”
Rh[inoceros]. frontalis von Martens, 1876:257. Type locality “Borneo.”

Rhinoceros karnuliensis Lydekker, 1886b:120, 121. Type locality “Karnul caves,” Karnul District, Madras, India; fossil from the late Pleistocene.

Rhinoceros karnuliensish Lydekker, 1886b:121. Incorrect subsequent spelling of *Rhinoceros karnuliensis* Lydekker, 1886b.
R[hinoceros]. annamiticus Heude, 1892:113, pl. XIXA, figs. 1 and 4. No type locality given; restricted to “Vietnam” by Groves and Guérin (1980:199).

Rhinoceros sivasondaicus Dubois, 1908:1245, 1258. Type locality “Kendeng [= Solo Valley],” Java; fossil probably from the Upper Pleistocene.

Rhinoceros [(Rhinoceros)] sondaicus: Lydekker, 1916:48. Name combination.

Aceratherium boschi von Koenigswald, 1933:121. Type locality “Java;” fossil from the late Pliocene (= *Rhinoceros sondaicus* fide Aimi and Sudijono 1979).

Rhinoceros sinhaleyus sinhaleyus Deraniyagala, 1938:234, 235, fig. 2. Type locality “Ratnapura series,” Sri Lanka; fossil probably from the Upper Pleistocene.

R[hinoceros]. Javanensis Barnard, 1932:185. Incorrect subsequent spelling of *Rhinoceros javanicus* É. Geoffroy Saint-Hilaire and F. Cuvier, 1824.

Rhinoceros sondaicus simplisinus Deraniyagala, 1946:162, fig. 2, pl. XXI. Type locality “Pothu kola Deniya, Nivitigala, near a tributary of the Hangamu ganga,” Sri Lanka; fossil probably from the middle Pleistocene.

R[hinoceros]. s[ondaicus]. floweri: Groves, 1967:234. Name combination.

R[hinoceros]. s[ondaicus]. inermis: Groves, 1967:234. Name combination.

E[urhinoceros]. sondaicus: Heissig, 1972:29. Name combination.

Rhinoceros sondaicus guthi Guérin in Beden and Guérin, 1973:19. Type locality “Phnom Loang (Province de Kampot, Cambodge [= Cambodia]);” fossil probably from the Pleistocene (Groves and Guérin 1980).

Rhinoceros sondaicus annamiticus: Groves and Guérin, 1980:199. Name combination.

Rhinoceros son daicus annamiticus Poleti, Van Mui, Dang, Manh, and Baltzer, 1999:34. Incorrect subsequent spelling of *Rhinoceros sondaicus* Desmarest, 1822.

CONTEXT AND CONTENT. Order Perissodactyla, suborder Ceratomorpha, family Rhinocerotidae, subfamily Rhinocerotinae, tribe Rhinocerotini, genus *Rhinoceros*. The specific type locality of *R. sondaicus* in Java is unknown (Rookmaaker 1982). The genus includes 2 species: *R. sondaicus* (Fig. 1) and *R. unicornis* (Indian rhinoceros—Grubb 2005). Morphologic data (Groves 1967, 1993, 1995a; Groves and Chakraborty 1983; Groves and Guérin 1980; Grubb 2005) and haplotypic uniqueness (Fernando et al. 2006) have been

used to distinguish subspecies of *R. sondaicus*. At the specific level, for example, mean antorbital width and ratio of the width to height of occiput are 204.0 mm and 175.6 mm: subspecifically, *R. s. annamiticus*, 217.7 and 181.0; *R. s. inermis*, 198.8 and 165.0; and *R. s. sondaicus*, 187.3 (Java) and 188.8 (Sumatra) and 186.0 (Java), 176.0 (Sumatra), and 171.0 (Malaya—Groves 1967, 1995a; Groves and Guérin 1980). *R. s. inermis* (Sunderbunds and Malaya) is no doubt extinct. *R. s. sondaicus* (West Java) and *R. s. annamiticus* (southern Vietnam and Cambodia) are extremely rare in their extant range (limited to 2 localities—Amin et al. 2006; Talukdar et al. 2009; van Strien et al. 2008) and extinct in all former ranges, making collection of additional specimens impossible; further assessments of materials in private collections and provincial museums are needed to clarify subspecific designations. Grubb (2005) recognized the following 3 subspecies:

R. s. annamiticus Heude, 1892. See above.

R. s. inermis Lesson, 1838. See above.

R. s. sondaicus Desmarest, 1822. See above.

NOMENCLATURE AND HISTORICAL NOTES. Along with skins and skeletal material, live wild animals were captured and shipped from all over the world in the 1700s and 1800s (e.g., Brandon-Jones 1997; Elliot and Thacker 1911), many to European menageries—some traveling and some stationary (Hoage et al. 1996). Rhinoceroses were particularly prized, and the Zoological Gardens of the Royal Zoological Society of London, established in 1828, paid £800 (U.S. equivalent today = \$77,800) for a *R. sondaicus* in 1874 and £1,000 (\$116,900) for a *R. unicornis* in 1834 (Sclater 1874, 1876b). An interesting case that affected the nomenclatural history of *R. sondaicus* was the “Javan Rhino in the Berlin Zoo” that also passed through the Zoological Gardens in London (Reynolds 1961; Sclater 1876b). William Jamrach, from a well-known family of “animal traders” in the mid-1800s (Brandon-Jones 1997), brought a rhinoceros from Manipur, India, to London in 1874. Jamrach was unsatisfied with its taxonomic identification as *R. sondaicus* by zoologists in London (Reynolds 1961), so he named it *Rhinoceros jamrachii* after himself in an unpublished report with no nomenclatural standing (Groves 1967; Sclater 1876b). This rhinoceros was shipped to the Berlin Zoo in 1874, and P. L. Sclater identified it there in 1879 as *R. unicornis* (Reynolds 1961). Groves (1967:234) included *R. jamrachii* Sclater, 1876b, as a questionable synonym of *R. sondaicus inermis*, but Grubb (2005:636) listed *R. jamrachii* Jamrach, 1875, as a synonym of *R. unicornis*. Unfortunately, the specimen and its records were lost to World War II, and because it was never definitively identified as *R. sondaicus* (Reynolds 1961; Rookmaaker 1980, 1998), we did not include the name *jamrachii* in our synonymy. Another captive specimen, called the “Liverpool Rhinoceros,” experienced a similar identity crisis from the 1830s (Reynolds

1960) until Rookmaaker (1993) concluded it was *R. unicornis* not *R. sondaicus*.

Our early perceptions of general characters of *R. sondaicus* had a curious evolution in science and art (Clarke 1986; Cole 1953; Rookmaaker and Visser 1982). As early as Roman times (Cole 1953), rhinoceroses were imported and held captive in Europe (Rookmaaker 1998). In 1515, the shipment of an Indian rhinoceros to Lisbon, Portugal, caused much ado throughout the continent, although it died in a shipwreck a year later on route to Italy as a gift to Pope Leo X (Clarke 1986); the animal was stuffed and presented to the Pope (Cole 1953). Based on sketches by others, the famous German artist Albrecht Dürer (1471–1528), who also designed armor, produced the still-familiar woodcut of the armored “Lisbon rhino” (Fig. 2a). More than 150 years later, a woodcut of the “Rhinocerote” of Java (Fig. 2b) appeared in Jacobus Bontius’ tome on the animals of Java (1658, published posthumously). Bontius (1596–1631) was a physician and naturalist and best known for his discovery of beriberi in Asia, later determined to be caused by a vitamin B₁ deficiency. He died 27 years before the publication of his natural history work in Java (Bontius 1658), and the editor, G. Piso, added the illustration shown here in Fig. 2b (Rookmaaker and Visser 1982). The similarity between Dürer’s illustration, clearly of a stylized Indian rhinoceros, and that in Bontius (1658) is striking (Clarke 1986), particularly the shape of the dermal shields, horn, and posture. Nevertheless, the Bontius illustration is less armored looking than Dürer’s and depicts a nape shield typical of *R. sondaicus* (Rookmaaker and Visser 1982) and, in our opinion, the extended upper lip, ears, visible tail in side profile, and epidermal patterning are more like the realistic early illustration of *R. sondaicus* in Horsfield (1824; Fig. 2c). The evolution from the novelty of Dürer’s woodcut to the realism of Horsfield’s illustration took almost 3 centuries (Clarke 1986; Cole 1953).

The generic epithet *Rhinoceros* means nose (*rhino*)-horn (*ceros*) in Greek, and the specific epithet *sondaicus* references the Sunda Islands (= Java) with the Latin locality suffix “*icus*.” Along with Javan rhinoceros (*rhino*), other common names include lesser Indian rhinoceros (19th century—Rookmaaker 2006); lesser one-horned rhinoceros; warak (Javanese); baduk or badak (Malay and Sundanese [western parts of Java]); gomda, ganda, genda, gainda, gomela, and gainra (Hindi); gonda (Bengali); kunda, kedi, and kweda (Naga); kyeng and kyan-tsheng, kyan-hsin or pyan-hsin, and meeza (Burmese); rhinoceros de la Sonde (French); and rinoceronte de Java (Spanish—Cole 1953; Evans 1905; Horsfield 1824; Lydekker 1907; U Tun Yin 1967; van Strien et al. 2008). More descriptive Malayan names include badak bersisih (= scaly rhinoceros) and badak tenggiling (= pangolin rhinoceros—Miller 1942). The 100th anniversary of the Museum Zoologicum Bogoriense (Java) was commemorated with a 700-rupiah stamp featuring *R. sondaicus*

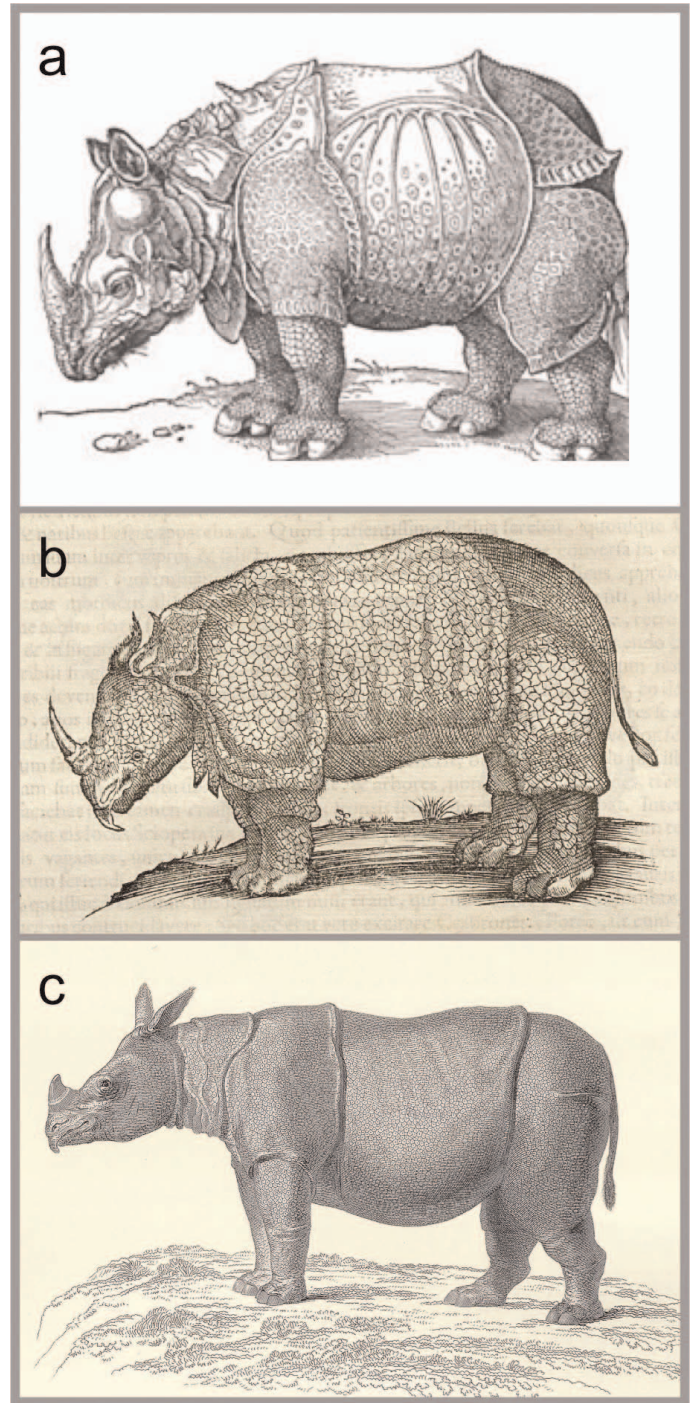


Fig. 2.—Early renditions of rhinoceroses involving our perception of *Rhinoceros sondaicus*: a, 16th century woodcut by German artist Albrecht Dürer of an Indian rhinoceros (*R. unicornis*) imported to Portugal in 1515; b, *R. sondaicus* from Java as depicted in Bontius (1658); and c, *R. sondaicus* from Java in Horsfield (1824), the most realistic of the 3 illustrations (if the electronic image is enlarged, the closely arranged epidermal polygons and nape shield are evident in panel c).

(Foose and van Strien 1995). In the late 1970s, the Indonesian 100-rupiah note carried the image of *R. sondaicus*.

DIAGNOSIS

Rhinoceros sondaicus is similar but generally smaller (Anonymous 1874; Blyth 1875; Lydekker 1907; Sclater 1874) than the Indian rhinoceros (Dinerstein 2011; Laurie et al. 1983). The skull of *R. sondaicus* is lighter than that of the Indian rhinoceros. In *R. sondaicus*, basal length of the skull is < 600 mm; maxillary toothrow length is < 241 mm; nasals are comparatively smooth, pointed, and rarely > 110 mm wide; and occiput from opisthion to inion is < 190 mm. In contrast to the Indian rhinoceros, premaxillae in *R. sondaicus* are narrow and (except in aged individuals) unfused to the maxillae and freely movable on them, and the vomer is thin and free from pterygoids except in very old individuals. Cheek teeth are not strongly hypsodont; crown heights of unworn M1–2 are 46–53 mm; parastyle buttress is pronounced; ectoloph is sinuous; crista is rudimentary or absent; protocone fold is absent; and at least a remnant of lingual cingulum is present on upper cheek teeth.

Skin folds are shallower on *R. sondaicus* than on the Indian rhinoceros (Anonymous 1874; Blyth 1875; Lydekker 1907); subcaudal folds fall short of the pelvis; posterior cervical folds follow a rounded, posterodorsal direction to meet behind the withers; and epidermal polygons are close and flattened, giving the skin a reticulated appearance. The form of the posterior cervical fold (lateral shoulder fold) in *R. sondaicus*, continuing up over the nape of the neck forming an independent shield shaped like a saddle, is diagnostic; in the Indian rhinoceros, the nape shield is continuous with the larger shoulder shield (Sclater 1874, 1876b:plates XCV and XCVI). Mature males do not develop the enlarged “bib” and deep cheek and neck folds of the Indian rhinoceros, at least not to the same degree. The tail of *R. sondaicus* stands out distinctly from the hindquarters, “so that its whole extent is exposed in a side view” (Lydekker 1907:25). In contrast to the Indian rhinoceros, intestinal villi of *R. sondaicus* are shorter and broader, and the caecum and colon are shorter (Beddard and Treves 1887).

GENERAL CHARACTERS

The genus *Rhinoceros* is distinguished by a single nasal horn; both upper and lower incisors are present, the lateral lower incisors being hypertrophied and tusklike; deciduous dentition has DM1; cheek teeth are subhypsodont; mediusinus of upper molars is of approximately equal depth to postsinus; and crochet of upper molars arises from apex of metaloph (Groves 1982b). The skull is short (Carter and Hill 1942; Peters 1878:tafeln 1–3), with the occipital plane inclined forward making the dorsal profile strongly concave;

postglenoid and posttympanic are fused below auditory meatus; orbitoaural length is greater than orbitonasal; infraorbital foramen is above P2; posterior edge of nasal notch is over P1 position; and auditory meatus is closed inferiorly by fusion of the post-glenoid and post-tympanic processes. The lacrimal bridge is usually ligamentous, and the antorbital process is ovate (Cave 1965). The skull of *R. sondaicus* relative to that of the Indian rhinoceros has unexpanded nasal bones not forming a nasal boss, less deepened dorsal concavity, premaxillae free from maxillae until old age, and a thin vomer free (until old age) from pterygoids. The maxillary molar and premolar teeth retain their π -like shape, unlike the Indian rhinoceros, and the buccal margins (ectolophs) are markedly sinuous, with prominent styles. Skin folds including scapular, pelvic, humeral, femoral, and subcaudal are pronounced (Figs. 1 and 2c). Processus glandis of the penis is located on either side of the dorsum of the glans, with a relatively long sessile anteroposterior attachment to glans and long narrow projection laterally (Cave 1965).

Few measurements of mass of *R. sondaicus* are available; 1 female, 1,500 kg; 1 male, 1,200 kg (Groves 1982a), and 1 exceptional specimen, said to be 2,280 kg (Sody 1959). Head-and-body lengths “over curves” are 305–344 cm, and shoulder heights are 120–170 cm, slightly higher at the rump than at the withers (Groves 1982a). Females may be slightly larger than males (Groves 1982a; Hoogerwerf 1970), but definitive conclusions are lacking (Groves 1995b). The nasal horn occurs on males, rarely on females (Lydekker 1907 cf. Groves 1982a), and is slightly curved backward. Length of the horn averages 20–25 cm (Groves 1982a) but may reach 30.5 cm straight and 36.9 cm on the curve (Finlayson 1950); a record length from Burma was shorter at 27.3 cm (Peacock 1933). The base of the horn is about 12 by 18 cm and narrows to 5.5 by 7.5 cm at the smooth part of the horn, beginning at about 8 cm above the base. The breadth of the stem is 40–50% of the breadth of the base, which shows fibrous ends in young *R. sondaicus*, but it becomes smoother, but grooved, with a broad, deep anterior longitudinal groove (as in Indian rhinoceros) in adults.

The color of the generally hairless hide of *R. sondaicus* is typically gray to dusky gray rather than brown (Lydekker 1907); the horn is black. The epidermal mosaic-like polygons on the skin resemble scales (Harper 1945; Lydekker 1907; Peacock 1933) and are clearest on limbs and detectable from some distance. Body hair is visible in young, but it virtually disappears in adults except for ear-fringes, eyelashes, and a tail-brush. Pedal scent glands are present, as in the Indian rhinoceros (Beddard and Treves 1887). The upper lip is long and flexible (almost prehensile).

DISTRIBUTION

Rhinoceros sondaicus is now apparently restricted to 2 localities (Fig. 3): the extreme western end of the island of



Fig. 3.—*Rhinoceros sondaicus* occurs in only 2 very small areas of southeastern Asia: Ujung Kulon, West Java (about 6°45'S, 105°15'E), and Cat Loc, Vietnam (about 11°35'N, 107°22'E; perhaps extinct). Green shading delimits areas of known historical distribution based on museum specimens collected beginning in the mid-1800s (Groves 1967; Rookmaaker 1980).

Java in Ujung Kulon National Park (Murphy 2004; World Conservation Monitoring Centre 2005) and Cat Loc in Cat Tien National Park in southern Vietnam (Santiapillai 1992; Schaller et al. 1990), if not now extinct in this latter locality. It once ranged throughout much of the central Indochinese subregion and the southwestern Sondaic subregion of southeastern Asia (Corbet and Hill 1992:map 106). Because of the critically endangered status of *R. sondaicus*, its general historical distribution and decline have been summarized repeatedly (e.g., Groves 1967; Harper 1945; Hoogerwerf 1970; Loch 1937; Rookmaaker 1980; Sody 1959). Lacking definitive records, we consider that generalized historical distribution of *R. sondaicus* (e.g., Foose and van Strien 1997; van Strien et al. 2008) to be overstated.

In Java, *R. sondaicus* was much more widespread and ascended volcanic mountains up to 3,300 m above mean sea level (Horsfield 1824; Sody 1959), but it is now isolated in the western coastal lowlands (Hoogerwerf 1970). Even in Ujung Kulon, a lowland rain forest, Ammann (1985) found that low-lying areas are used more than higher ground. In

Sumatra, the last known individuals were killed between 1927 and 1933 (de Beaufort 1928; Hazewinkel 1933; Sody 1959; Vageler 1927). *R. sondaicus* was never known to occur in Borneo in recent times, but fossils from the late Pleistocene–early Holocene have been found (Cranbrook 1986), and some evidence suggests they may have survived there until the 10th century, perhaps longer (Cranbrook and Piper 2007). *R. sondaicus* was very uncommon or extinct in Malaya by the 1930s (Comyn-Platt 1937; Fetherstonhaugh 1951; Page 1934); the last known individual was shot in Kroh Forest, Perak, in 1932. Prior to that time, it was not found east of the north–south mountain range that divides the Malay Peninsula (Harper 1945), and it was extinct in the Telok Anson District where it had once occurred (Morris 1935). The supposed rediscovery of *R. sondaicus* in Malaya in the 1950s (Ali and Santapau 1958) was based on a photograph of a Sumatran rhinoceros (*Dicerorhinus sumatrensis*—Groves and Kurt 1972) with an extremely small 2nd horn.

In Thailand, Loch (1937) gives Krabin as a former locality of *R. sondaicus*. In the 1970s, it was still reported by local villagers in the Tenasserim Range of southwestern Thailand (McNeely and Cronin 1972; McNeely and Laurie 1977). In Burma (= Myanmar), *R. sondaicus* was common in the mid-1800s (Mason 1882), uncommon by the end of the century (Evans 1905), and very uncommon by the 1920s (Ansell 1947; Blanford 1939); 6 individuals were said to exist in the Kahilu Game Sanctuary in the 1930s (Thom 1935); at least 2 *R. sondaicus* were consistently reported on the Thaton–Pegu border from 1939 to 1949; 1 individual was shot on the Tavoy–Amherst border in 1954 (U Tun Yin 1954, 1956); and 2 individuals possibly occurred in the Tavoy region on the Burma–Thailand border in 1958–1962 (McNeely and Cronin 1972; Milton and Estes 1963). A single individual was encountered by poachers near the Burma–Thailand border in 1958; a pregnant female was killed there and another individual was encountered in 1960 (McNeely and Cronin 1972); a few individuals may have survived after that in the northern sector of the Tenasserim Yoma within Kawthulei State and Moulmein (formerly Amherst) District (U Tun Yin 1967). According to Peacock (1933), *R. sondaicus* never occurred outside of the former Thaton, Salween, and Mergui forest divisions of Burma (= peninsular parts of Burma), where it inhabited heavy evergreen forests on relatively flat ground (Groves 1967).

Rhinoceros sondaicus was well known in Laos and Cambodia (Flower 1900; Harper 1945; Rookmaaker 1980). Although Rookmaaker (1988) thought that a few individuals may occur there, none have been found recently (Daltry and Momberg 2000; Talukdar et al. 2009). In Cambodia, it is depicted on bas-reliefs at Angkor Wat (de Jongh et al. 2005), and the last known individual was shot on the Chup Plateau, Kampong Cham Province, in May 1930 (Poole and Duckworth 2005). In Vietnam and Laos, it may have

occurred up to the Chinese border, but definitive specimens are lacking (Rookmaaker 1980:figure 2). Over much of this area, the Indian rhinoceros is the only rhinoceros species said to have occurred there, but *R. sondaicus* is known from Cochin China in southern Vietnam (Groves 1967; Harper 1945; Rookmaaker 1980).

Rhinoceros sondaicus is the only rhinoceros known to have occurred in the Sunderbunds of India and Bangladesh (Rookmaaker 1980, 1997, 2006). Its presence there was confirmed up until the late 1800s (Burton 1951). In January–February 1892, de Poncins (1935) estimated that 3 or 4 individuals probably existed on 5 islands; he saw 1 individual but refused to kill it. Harper (1945) mentioned the occurrence of *R. sondaicus* in Orissa, the Mahanadi delta, and the Jalpaiguri forest. Higgins (1935) suggested that *R. sondaicus* occurred in the Manipur Hills in the early 1930s, but he could not corroborate that with personal observations. Given that the identity of a captive specimen from the Manipur Hills in 1874, initially referred to as *R. sondaicus* and then as an Indian rhinoceros, is in doubt (Reynolds 1961), the presence of the former species there remains unproven. It did, however, occur at Moraghat, in the Jalpaiguri district of northern West Bengal, as verified by 1 female specimen in the Copenhagen Museum (Rookmaaker 2006); here, it was apparently sympatric with the Indian rhinoceros, of which there also is a skull from the same locality, now in Copenhagen.

FOSSIL RECORD

The evolution of rhinoceroses spans 50 million years, and fossil evidence of ≥ 60 genera and hundreds of species exist—forms that “occupied nearly every niche available to large mammalian herbivores” (Cerdeño 1995; Dinerstein 2003, 2011; Prothero 1993:82; Prothero et al. 1986). Rhinocerotoids dominated large land mammalian faunas from 34 million years ago until the “mastodonts escaped from Africa about 18 million years ago” (Prothero 1993:82). The common ancestor of extant species of rhinoceroses may date from 28 to 33 million years ago with the next divergence within the group occurring only 1.0–1.5 million years later (Willerslev et al. 2009 cf. Tougaard et al. 2001).

According to Hooijer (1949:126), *R. sondaicus* changed “from a swift-moving to a slow-moving animal during the Quaternary” but not as evolved as the Indian rhinoceros (Hooijer 1946a). Fossil remains of *R. sondaicus* from the early and middle Pleistocene have been found in Java (Sangiran, Ngandong, and other sites—Hooijer 1964), middle Pleistocene from Malaya (Hooijer 1962a), middle Pleistocene from northern Vietnam (Bacon et al. 2004), and probable Pleistocene from Cambodia (Beden and Guérin 1973). The Javanese fossil race was less graviportal with longer distal limb segments than extant *R. sondaicus* (Hooijer 1949). Subfossil remains are known from Sumatra (Hooijer 1948),

Borneo (Cranbrook 1986; Cranbrook and Piper 2007), Malaya (Hooijer 1962b), and Java (Dammerman 1934). During the Pleistocene, *R. sondaicus*, or precursors, occurred in India and Sri Lanka (Chauhan 2008; Deraniyagala 1937, 1938, 1946; Lydekker 1877, 1886a, 1886b; Manamendra-Arachchi et al. 2005), well beyond its current distribution (Fig. 2). Hooijer (1946b) concluded that *R. karnuliensis* was similar to *R. sondaicus*. *R. sinhaleyus* (= *R. sondaicus simplisinus*) also was probably conspecific, although no doubt subspecifically distinct. Neolithic remains have been described from Cambodia (Guérin and Mourer 1969).

FORM AND FUNCTION

Relatively few museum specimens of *Rhinoceros sondaicus* exist for comparisons (Barbour and Allen 1932; Loch 1937). Groves (1967:tables 4 and 5) provided various skull and teeth measurements of recent specimens by country of origin and comparisons with Pleistocene and subfossil specimens. Although sample size was relatively small, representative mean basal skull lengths (mm \pm SD) were: Java, 575.8 \pm 14.1 ($n = 9$); Sumatra, 578.4 \pm 14.3 (5); Malaya, 506.5 \pm 10.6 (2); Vietnam, 525.0 \pm 2.8 (2); and Bengal, 567.3 \pm 17.5 (3).

In contrast to other genera of rhinoceroses (Groves 1971), the base of the horn in *Rhinoceros* rises rapidly, in ontogeny, above dorsum nasi, with a broad, irregularly grooved basal zone; the original tubercular knob becomes smooth as the epidermal polygons fuse together with continuous keratinization; a specimen is known with a scaleless epidermal field several centimeters behind the horn, possibly representing an incipient frontal horn (Neville 1927). The horn is said to be totally lacking in female *R. sondaicus* from the Sunderbunds (de Poncins 1935; Fraser 1875; Sclater 1876a) and probably Sumatra (Vageler 1927), but in some populations, it occurs in females as a small tuberosity (Ammann 1985; Barbour and Allen 1932; Neville 1927; Schuhmacher 1967). One female skull from Tenasserim in the Natural History Museum (London), specimen 1921.5.15.1, has a horn 19.2 cm long.

Rhinoceros sondaicus is generally said to be hairless, although a sparse hairy covering has been noted (Cave 1969; Groves 1967); the female specimen from Tenasserim mentioned above is decidedly hairy. Hairs are probably abraded and lost with age, as is the case with other rhinoceros species. Another specimen in the Natural History Museum (London) (1932.10.21.1) lacks visible hair, and because it was superbly mounted, loss of any hair during mounting seems unlikely. Epidermal polygons are flat and closely arranged, so that parts of the hide appear divided by a network of cracks (Fig. 2c). Skin thicknesses of *R. sondaicus* vary from 2.5 to 3.5 cm depending on the location on the body (Sody 1959).

Using an age-based sequence of the increasing 3-toed footprint size of Indian rhinoceroses in the Basel Zoo,

Switzerland, Hoogerwerf (1970) developed a system to differentiate sexes and young of *R. sondaicus* in Ujung Kulon. That classification provided insight into productivity and sex ratios and has been followed by others (e.g., Poleti et al. 1999; Sadjudin 1987; Santiapillai et al. 1993a, 1993b; Schenkel and Schenkel-Hulliger 1969a). Forefoot prints of adult *R. sondaicus* are up to 32 cm wide (Hoogerwerf 1970), which is as large as the Indian rhinoceros. Toes (= hooves) are less prominent and soles are more extensive than in the Sumatran rhinoceros (van Strien 1978). Despite the purported greater size of female than male *R. sondaicus*, footprints of males are larger than those of females, which were never > 28 cm (Hoogerwerf 1970). Ammann (1985) gives the following forefoot widths: adult males, 26–29 cm ($n = 5$); adult females, 25–27.5 cm (7); and immature, < 24 cm.

The premaxillae have long, slender, preincisive processes (Fig. 4); they fuse with the maxillae late in life or not at all; I1s are lost in old age (Pocock 1944). A partially ossified nasal septum occurs, particularly in museum specimens of *R. s. inermis* from the Sunderbunds (Fraser 1875; Pocock 1945a). The skull of *R. sondaicus* is small and lighter than that of the Indian rhinoceros (Laurie et al. 1983); there is less nasal expansion, and the horn base is generally pointed rather than rounded; the ascending ramus is less elongated; the occiput is comparatively low and broad, giving a shallower dorsal profile to the skull as a whole; the posterior margin of the palate has a pronounced median projection; the basilar region is broad; the pterygoids usually are more laterally expanded; and the vomer is thin and free from the pterygoids, except in old age when they may fuse with the floor of mesopterygoid fossa (Colbert 1942; Pocock 1945b). The lacrimal bridge remains ligamentous in 83% of skulls (Cave 1965).

Typical of most Perissodactyla, the mandible of all species of rhinoceros is robust (Fig. 4), and the cheek teeth are double-crescent (Fig. 5). The large, procumbent, tusklike lateral incisors (sometimes incorrectly called canines) are characteristic of the 3 Asian rhinoceroses (cf. Groves and Kurt 1972; Laurie et al. 1983). Only members of the genus *Rhinoceros* have a pair of central incisors; these are very small compared with the lateral incisors, with short and slender roots, and are often lost during museum preparation (Fig. 5).

Dental formula of *R. sondaicus* is $i\ 2/2, c\ 0/0, p\ 3/3, m\ 3/3$, total 32 (Fig. 2); deciduous dental formula is $i\ 2/2, c\ 0/0, m\ 4/4$. The teeth of *R. sondaicus* are more brachyodont than in the Indian rhinoceros; the ectoloph is strongly sinuous because of the prominence of the parastyle buttress; a crista generally is absent, or very small; medifossettes and postfossettes are only rarely formed; a protocone fold is absent; and there commonly is a tubercle or remnant of a cingulum at the entrance to the median valley (Groves 1982b). Unlike the Indian rhinoceros, crowns of cheek



Fig. 4.—Ventral, dorsal, and lateral views of skull and lateral view of mandible of a mature male *Rhinoceros sondaicus* (Natural History Museum [London] specimen 1876.3.30.1) collected in the Sunderbunds, West Bengal, India, in 1876. Greatest length of skull is 523 mm.



Fig. 5.—Dorsal (left) and ventral (right) views of the mandible of an adult *Rhinoceros sondaicus* (Natural History Museum [London] specimen 1876.3.30.1); note the large tusklike lateral incisors, characteristic of Asian rhinoceroses, and the 2 alveoli for the missing small central incisors (right mandible), characteristic of the genus *Rhinoceros*.

teeth of *R. sondaicus* “wear into ridges instead of a uniformly flat plane,” suggesting a browse diet (Lydekker 1907:35).

One of us (C. P. Groves) determined the following from examination of new skeletal material in the Natural History Museum (London). Length of the radius is 82.7% (range = 81–84%) of the length of the humerus; length of tibia is 73.3% (70–75%) of the femur and 98.3% (98–99%) of the radius; and length of the humerus is 90.3% (89–91%) of the femur. Total forelimb length is 97.7% (97–98%) of hind-limb length; length of the humerus is 79.7% (73–84%) of the basal length of the skull, and metacarpal III is 53.8% (53–55%) of the length of the radius. Vertebral formula is 19 T, 3 L, 5 S, and 22 Ca; vertebral morphology in *R. sondaicus* is similar to that of the Indian rhinoceros.

The brain of *R. sondaicus* is similar to that of the Indian rhinoceros (Beddard and Treves 1887). The stomach of *R. sondaicus* is more similar to that of the Sumatran rhinoceros than the Indian rhinoceros. Villi begin 75 mm along the duodenum; they are shorter and broader than in the Indian rhinoceros (Beddard and Treves 1887). The bile duct opens 18 cm from the pyloric sphincter. The caecum is short, blunt, and 61 cm long and 51 cm wide in adult *R. sondaicus* and 38 by 30 cm in young. Submucous caecal glands found in the Sumatran rhinoceros are apparently absent in *R. sondaicus* and the Indian rhinoceros (Cave and Aumonier 1963). The ileocaecal fossa is of a size “capable of engaging the entire fist” (Beddard and Treves 1887:193). The colon, including the rectum, is 44 cm long—less than in other Asian rhinoceroses—and it is folded in a loop with a mesentery uniting the opposite sides of the loop and fed by a branch of

the colic artery. The liver is 5-lobed; the right central lobe is larger than the right lateral lobe; the caudate lobe is 53 cm long; and the spigelian lobe is small, 12.7 cm long by 3.8 cm wide (Beddard 1889; Beddard and Treves 1887; Garrod 1877a).

The uterus of *R. sondaicus* is bicornuate, each horn in a young female being 205 mm long; the corpus uteri is 75 mm long (Garrod 1877a). Seminal vesicles are slender tubes, closely adherent to the prostate (Beddard and Treves 1887). Processus glandis of *R. sondaicus* is lobular as in the Indian rhinoceros (Laurie et al. 1983).

ONTOGENY AND REPRODUCTION

Gestation length of *Rhinoceros sondaicus* is unknown, but the congeneric Indian rhinoceros gestates for 462–491 days (Dinerstein 2003, 2011; Hayssen et al. 1993; Laurie et al. 1983). Both species have a single offspring. A fetus of *R. sondaicus*, thought to be halfway through gestation, was about 17 cm long with a well-developed skin pattern (Frechkop 1951). Basal lengths of skulls of young with their full complement of milk teeth average 65.6% of adult skulls; when the M1 crypt opens, basal lengths of skulls of young are 75–77% that of adults. Occipitonasal length decreases with age from 95% to 89% relative to basal length; zygomatic breadth decreases from 69.5% to 60.4%, without a subsequent increase in adult *R. sondaicus* as in the Indian rhinoceros, which tends to develop rugosity on the angle of the zygomatic arch (lacking in *R. sondaicus*). Nasal breadth in female *R. sondaicus* does not increase after the 1st appearance of M1 when the horn (if any) evidently reaches adult size; nasal breadth in male *R. sondaicus* continues to increase, reaching only 83% of its maximum after 1st appearance of M1. A skull of *R. sondaicus* from a zoo specimen was remarkably small, suggesting considerable ability to remain stunted under adverse conditions, as in the Indian rhinoceros (Groves 1982b).

A “very” young *R. sondaicus* was 130 cm at the shoulder; after 4 years and fully grown, it was 170 cm (Horsfield 1824). Shoulder height of the Indian rhinoceros is 130 cm at 1.5–2 years of age, suggesting that *R. sondaicus* is full grown at 5.5–6 years of age, earlier than the Indian rhinoceros. Footprints of the forefeet of female *R. sondaicus* accompanied by young may be only 25 cm wide, suggesting that they start breeding at somewhat over 4 years (Ammann 1985). The birth interval of *R. sondaicus* is said to be 4–5 years, and weaning occurs at 12–24 months (Rinaldi et al. 1997). Likely somewhat comparable to *R. sondaicus*, congeneric male Indian rhinoceroses are reproductively active by 7 years; females are polyestrous and 1st estrus occurs at 4 years; estrous cycle length varies from 24 to 126 days; 1st parturition is at 6–8 years (Dinerstein 2003, 2011; Hayssen et al. 1993—mostly information from captive individuals).

ECOLOGY

Because of the extreme rarity and highly protected status of *Rhinoceros sondaicus*, few contemporary ecological and behavioral studies have been conducted because they could be disruptive. The greatest insight on *R. sondaicus* in Ujung Kulon was provided by Sody (1959) based on his long residency as an agricultural teacher in Java (1918–1947); by Hoogerwerf (1970) when he worked there, with some intermittency due to war and foreign occupation, in 1937–1957; by Schenkel and Schenkel-Hulliger (1969a) based on their fieldwork in Ujung Kulon in 1967–1969; and by Ammann's (1985) doctoral work in 1978–1980. Unless otherwise noted, the summary that follows represents research on *R. s. sondaicus* in Ujung Kulon, West Java, rather than *R. s. annamiticus* at Cat Loc, Vietnam, where little ecological information exists because of the population's relatively recent discovery (Schaller et al. 1990) and extremely low numbers (Murphy 2004; Poletti et al. 1999; Santiapillai et al. 1993a, 1993b).

Population characteristics.—By the 1930s, range-wide estimates of the numbers of *Rhinoceros sondaicus* were as low as 66 (Loch 1937). The small size of the 2 extant populations of *R. sondaicus* and difficulty obtaining observations in the field make it impossible to know what the normal population demography was or should be. At a time when the Ujung Kulon population seemed to be increasing, Ammann (1985) found that tracks of immature *R. sondaicus* were 6.5–7.5% of the total tracks counted in 1978 and 15.9–17.2% in 1980, and he considered these to be minimum figures because he saw no tracks < 22 cm.

In Vietnam, only 2–6 individuals questionably remain with no known reproduction since 1997 and no confirmed male in the remnant population (Murphy 2004); they are relegated to suboptimal habitat disjunct from preferred riparian areas (Polet and Ling 2004). Van Strien et al. (2008) considered the Vietnamese population as no longer viable, and it may now be extinct. In Ujung Kulon, sex ratios inferred from 219 direct observations in various periods from 1940 to 1954 were highly skewed toward males (222 males:100 females—Hoogerwerf 1970), which paralleled observations in 1967–1968 by Schenkel and Schenkel-Hulliger (1969a), although Ammann (1985) could not exclude a 1:1 sex ratio. In contrast, sex ratios of Indian rhinoceroses in Nepal are generally equal to sometimes favoring females (Dinerstein 2003).

No specific information exists on longevity of *R. sondaicus* in the wild, although Hoogerwerf (1970:127) opined that maximum age was “perhaps ... 30 or 40 years.” One individual lived 21 years in captivity at the Adelaide Zoological Gardens, Australia, and died in 1907 (Dover 1932; Finlayson 1950; Jones 1993; Weigl 2005). Two other captive individuals with records lived 11 years at the London Zoo and 14 years at the Calcutta Zoo (Dover 1932). An additional individual, captive in the early 1900s likely at the

Belle Vue Zoological Gardens, England, and identified as *R. sondaicus* from his skull, apparently lived to an advanced age based on evidence of periodontal and temporomandibular deterioration, not observed in wild specimens (Cave 1985).

Space use.—Early accounts about *Rhinoceros sondaicus*, when it was more numerous and widespread, suggest that it used a variety of habitats and localities (Blyth 1862; Horsfield 1824; Lydekker 1907; Mason 1882; U Tun Yin 1967). Horsfield (1824:unpaginated) noted that *R. sondaicus* was not limited by region or climate with “its range extend[ing] from ... ocean to the summit of mountains of considerable elevation” and typically with “a profuse vegetation.” Lydekker (1907:36) chronicled, “the Javan rhinoceros prefers forest tracts to grass-jungles, and is generally met with in hilly districts, where it apparently ascends in some parts of its habitat several thousand feet above sea-level.”

If current preferences of *R. sondaicus* are indicative, it was probably most abundant in lowland forests and fertile floodplains, as were common in West Java, and it was largely absent from dense upland forests throughout its range (e.g., eastern Java, northern Thailand, and Laos—Groves 1967; Ramono et al. 1993, 2009). Ammann (1985) considered its optimal habitat to be a mosaic of open glades within rain forest. In Ujung Kulon, *R. sondaicus* now uses primarily second-growth forests (Ammann 1985; see video at <http://www.arkive.org/javan-rhinoceros/rhinoceros-sondaicus/video-so00.html>, accessed 15 September 2010) with various degrees of the invasive palm, lang kap (*Arenga obtusifolia*—Ramono et al. 2009), which can be thinned to improve availability of tree saplings preferred by *R. sondaicus* (Putro 1997; Schenkel et al. 1978). *R. sondaicus* regularly visits coastal beaches in Ujung Kulon but avoids reef areas (Hoogerwerf 1970).

Rhinoceros sondaicus appears to wander extensively throughout its remaining range in Ujung Kulon, perhaps related to limited forage availability (Ammann 1985; Schenkel and Schenkel-Hulliger 1969a). From 16 tracking sequences, Ammann (1985) calculated that *R. sondaicus* in Ujung Kulon traveled 0.4–3.8 km/24 h. Hoogerwerf (1970) noted perennial paths worn throughout the forest there. Individual home ranges were not exclusive in Ujung Kulon (Rinaldi et al. 1997); Ammann (1985) found that those of females overlapped considerably, although those of males, at least the males that left sufficient traces of their presence, overlapped very little, and might actually be exclusive territories. Similarly, dominant male Indian rhinoceros use “temporally or spatially distinct home ranges” and females’ home ranges throughout the year (Dinerstein 2003:111).

Maxwell (1907) suggested that 1 male *R. sondaicus* used an area of about 100 km², much larger than the average annual home ranges of 3–5 km² of Indian rhinoceroses (Dinerstein 2003; Laurie et al. 1983). Ammann (1985) found that in Ujung Kulon, 4 females occupied home ranges of 2.61–8.4 km², and 3 males of 12.5–26.4 km² (perhaps as

much as 30 km²). One of the female's home ranges also was occupied by 2 other females. Ammann (1985) considered it likely that there are "strong" (= dominant) and "weak" (= subordinate) males, as in Indian rhinoceros (Dinerstein 2003; Laurie et al. 1983), and that strong males occupied territories and squirted urine to mark them much more than did weak males. Groves (1982a) calculated densities of *R. sondaicus* in Ujung Kulon at 0.14 individuals/km², which he surmised represented carrying capacity, in contrast to 0.45–1.79 individuals/km² for Indian rhinoceroses; however, Ammann (1985) found an average density, at least in his Javan study area, of 0.47–0.51 individuals/km². With only remnant numbers of *R. sondaicus* in Vietnam, density estimates are extremely low at only 0.01–0.03 individuals/km² (Santiapillai et al. 1993b; Schaller et al. 1990).

Diet.—*Rhinoceros sondaicus* is a generalist browser and consumes little to no grass and few herbaceous species, preferring leaves, shoots, and twigs of woody species (Ammann 1985; Hoogerwerf 1970; Pratiknyo 1991; Santiapillai et al. 1993a, 1993b; Schenkel and Schenkel-Hulliger 1969a; Sody 1959). Most of the insight on diets of *R. sondaicus* comes from evidence of browsing on plants and fecal analyses rather than assessments of stomach contents, or even direct observations, which are relatively uncommon. *R. sondaicus* forages most often in "thick scrub jungle or heavy secondary forest" but often frequents riverine and coastal areas and associated vegetation in Ujung Kulon (Hoogerwerf 1970:109). Parts of staple tree saplings consumed are typically 3–7 years old and 3–10 m high (Schenkel et al. 1978). Schenkel and Schenkel-Hulliger (1969a) listed 95 plants eaten by *R. sondaicus*, Hoogerwerf (1970) listed 71 plants, and on the higher end, Sadjudin (1984 not seen, cited in Ramono et al. 2009) listed 166 plants from 61 families and 127 genera. Ammann (1985) listed 190 species in the diet of *R. sondaicus*, of which just 4 made up 44% of the diet.

Tree species, particularly their saplings, and woody shrubs in second-growth forests dominate selected food items of *R. sondaicus* in West Java and include especially *Spondias pinnata*, *Amomum*, *Leea sambucina*, and *Dillenia excelsa* (Ammann 1985). Hoogerwerf (1970) mentions *Glochidion zeylanicum*, *Desmodium umbellatum*, *Ficus septica*, *Pandanus*, *Lantana camara*, and *Vitex negundo*—only 1 of which is in Ammann's list (at least at species level). Ammann (1985) noted that a large number of species of climbers were in the diet. *R. sondaicus* eats plants that have significant defenses against herbivory such as spines and thorns; Hoogerwerf (1970:105) noted that swamp thistle (*Acanthus ilicifolius*) and randu leuweung (*Gossampinus heptaphylla*) were eaten "without demur." While fruits such as those of kawung palm (*Arenga pinnata*), papaya (*Carica papaya*), and kemlandingan (*Leucaena leucocephala*—Hoogerwerf 1970) have been found in feces, they do not seem to form an important part of the diet of *R. sondaicus* (Ammann 1985), in contrast to Indian rhinoceroses in Chitawan National Park, Nepal, which relish fruits of the ubiquitous



Fig. 6.—Male *Rhinoceros sondaicus* reaching for forage in a glade in Ujung Kulon National Park, West Java; reach of the prehensile upper lip is potentially increased by the mobility of the premaxillae in all but the most-aged adults; dermal neck folds and body shields are evident. Photograph by Foad, Yahya & Sumiadi/World Wildlife Fund Indonesia used with permission.

riparian tree *Trewia nudiflora* (Dinerstein 1991, 1992; Dinerstein and Wemmer 1988). Some mineral requirements may be satisfied by the consumption of halophytes or plants growing along the seashore, or even by drinking seawater or brackish water, which have been recorded (Ammann 1985). In Vietnam, limited analyses of undigested material in feces suggested consumption of woody species, *Acacia pennata*, *Calamus tetradactylus*, *C. poilanei*, *Bambusa procera*, and *B. blumeana*, with evidence of wood-fern, *Cyathea*, and poisonous *Strychnos nux-vomica* (Santiapillai et al. 1993b).

Rhinoceros sondaicus appears to forage mostly at night (Hoogerwerf 1970; Horsfield 1824), and it will go to some length to obtain its preferred meal. It uses its chest, shoulders, neck, and chin to bring foliage into reach, grabbing it with its flexible upper lip (Hoogerwerf 1970; Fig. 6). The height of such "pushing marks [on forage typically] varied from 160 to 180 cm" to a maximum of 217 cm on *Ardisia humilis*, 250 cm on *D. umbellatum*, and 256 cm on *G. zeylanicum* (Hoogerwerf 1970:107). Diameters of uprooted and broken stems from foraging activities of *R. sondaicus* in Ujung Kulon were 10–15 cm but sometimes up to 25 cm; thicknesses of browsed twigs were usually 11–17 mm but up to 20 mm on *F. septica* and *Dillenia indica*, 25 mm on *V. negundo*, and even 45 mm on *G. heptaphylla* (Hoogerwerf 1970; Schenkel and Schenkel-Hulliger 1969a). It is possible that such use of the understory (browsing and

trampling), and perhaps dissemination of seeds in feces (cf. Dinerstein 1991, 1992), shaped some forest structures before numbers of *R. sondaicus* were so reduced (Groves 1982a).

Diseases and parasites.—Ectoparasites do not appear to be very common on *Rhinoceros sondaicus*, but only a few individuals have been examined. Ticks (*Amblyomma crenatum*) and biting horseflies (*Tabanus brunneus*) have been reported on *R. sondaicus* (Ammann 1985; Anastos 1950; Bequaert 1933; Palmieri et al. 1980). Sandground (1933) identified only 2 helminths (nematode *Kiluluma vernayi* and cestode *Anoplocephala diminuta*) in a single specimen of *R. sondaicus*. Three nematode (*Strongyloides*, *Bunostomum*, and *Trichostrongylus*), 2 trematode (*Fasciola* and *Schistosoma*), and 5 protozoan genera (*Balantidium*, *Entamoeba*, *Eimeria*, *Cycloposthium*, and *Lavieraella*) were found in feces collected in Ujung Kulon, Java; infestations were considered mild (Tiuria et al. 2006 cf. Palmieri et al. 1980). One early observation of the tapeworm *Taenia gigantea* was made by Garrod (1877b). With so few *R. sondaicus* remaining, disease is a monumental threat (Ramono et al. 2009); the death of 5 individuals in Ujung Kulon in the early 1980s was anecdotally thought to be caused by anthrax (Anonymous 1982).

Interspecific interactions.—A preference of *Rhinoceros sondaicus* for swampy areas likely minimized competitive interactions with the Sumatran rhinoceros, which prefers uplands (Groves 1972, 1982a; Ramono et al. 1993), but the 2 species are no longer sympatric because of their rarity and isolated distributions. The herbivorous bovid, the banteng (*Bos javanicus*), can be sympatric with *R. sondaicus* and could have been a potential competitor (Hoogerwerf 1970; Rinaldi et al. 1997). Today, the banteng is vulnerable or endangered throughout its remaining range (Leslie 2011; Manh 2009; Pedrono et al. 2009; Pudyatmoko et al. 2007; Timmins et al. 2008), and, typical of the genus *Bos*, it prefers a grass-dominated diet and drier open habitats under ideal conditions (Hoogerwerf 1970; Steinmetz 2004). Currently, the banteng population in Ujung Kulon National Park is estimated at 200–800 individuals (Alikodra 1987; Ashby and Santiapillai 1988; Timmins et al. 2008; World Conservation Monitoring Centre 2005), and ongoing concern over its effects on *R. sondaicus* has been expressed (Rinaldi et al. 1997), although it was not considered a serious potential competitor by Ammann (1985). The barking deer or muntjac (*Muntiacus muntjac*) is predominately a browser like *R. sondaicus*, but it also has declined in numbers in Java making competitive interactions unlikely (Hoogerwerf 1970). Rusa (*Rusa timorensis*), wild boar (*Sus scrofa*), and monitor lizards (*Varanus salvator*) use wallows created by *R. sondaicus* in Ujung Kulon (Hoogerwerf 1970). The Javan warty pig (*Sus verrucosus*), an unlikely competitor of *R. sondaicus*, is endangered, and no longer occurs in Ujung Kulon (Blouch 1988; Ramono et al. 1993).

Evans (1905) noted that *R. sondaicus* and Sumatran rhinoceroses were fearless of Asian elephants (*Elephas maximus*—Shoshani and Eisenberg 1982) and tigers

(*Panthera tigris*—Mazák 1981; Sunquist and Sunquist 2009). Aside from humans, an adult *R. sondaicus*, as with other rhinoceroses (Dinerstein 2011; Hillman-Smith and Groves 1994; Laurie et al. 1983), has no regular predators. Indian rhinoceroses < 6 months of age may be preyed on by tigers, but the subspecies of the tiger (*P. t. sondaica*—Sunquist and Sunquist 2009) that once occurred on Java is extinct (Ramono et al. 1993), so *R. sondaicus* in Ujung Kulon is not similarly affected.

HUSBANDRY

Captive-breeding programs have been proposed repeatedly for *Rhinoceros sondaicus* (Ammann 1985; Santiapillai and Suprahman 1986) but not without detractors (MacKinnon and Santiapillai 1991; Pramono 1991), and no action in this regard has been undertaken. Considerable knowledge exists about the history of captivity (Rookmaaker 1998) and husbandry of other species of rhinoceroses (Jones 1979). Nevertheless, virtually nothing is known about the husbandry of *R. sondaicus*—only 9–14 individuals have ever been held in captivity outside of Java (Reynolds 1960, 1961; Rookmaaker 1998). In the 1800s and before, accounts exist of *R. sondaicus* having a docile nature, wandering around villages, and being held captive for pleasure by country rulers (Horsfield 1824; Sody 1959).

The last known captive *R. sondaicus* lived at the Zoological Gardens in Adelaide, Australia, and died in 1907; it was exhibited as an Indian rhinoceros for most of its 21 years in captivity (Jones 1993; Reynolds 1960; Weigl 2005). Lengthy captivity of a male *R. sondaicus* in the early 1900s apparently resulted in deterioration of teeth and mandibles (Cave 1985). In a curious case, a *R. sondaicus* was shipped to the King of Klungklung, Bali, held captive from 1839 to 1842, and sacrificed and eaten during the King's postcremation ritual (Rookmaaker 2005).

BEHAVIOR

Grouping behavior.—Because so few *Rhinoceros sondaicus* exist in the wild, current grouping behavior is likely marginalized relative to what it once was (Fernando et al. 2006). Early accounts speak of a gregarious nature and large aggregations (Horsfield 1824; Santiapillai et al. 1993a, 1993b; Schaller et al. 1990). As early as the 1700s, bounties were paid in Java because of crop depredation; bounty records between 1 September 1747 and 14 January 1749 showed that 526 *R. sondaicus* and 80 Javan tigers were killed, causing suspension of the bounty system because of its exorbitant cost (Hoogerwerf 1970; Sody 1959). Currently, *R. sondaicus* is mostly solitary, “liv[ing] as independent or loosely associated nomads” (Schenkel and Schenkel-Hulliger 1969a, 1969b:69). It also occurs in small groups of a female and her offspring; a female, her older offspring, and a

male during mating (a relatively rare observation); and occasional pairs of just males or just females (Ammann 1985; Hoogerwerf 1970:plates 20–24; Rinaldi et al. 1997; van Strien and Rookmaaker 2010).

Reproductive behavior.—The reproductive repertoire of *Rhinoceros sondaicus* has not been observed. Hoogerwerf (1970:132–136) recounted rare episodes, presumed to be associated with rut, where female and male *R. sondaicus* “skirmished,” “sparred,” or “fought.” Such episodes were associated with loud roaring (thought to be the prelude to mating by Hoogerwerf [1970]), considerable destruction of vegetation in the area, and evidence of chasing; 1 episode extended over 200 m of beach. Both sexes of other species of rhinoceroses, free-ranging and in captivity, are known to engage in vigorous mating rituals in rut, sometimes resulting in serious injury (Dinerstein 2003; Hoogerwerf 1970). In 2 cases where a male and a female *R. sondaicus* travelled together, they moved only 605–936 m in 24 h, much less than solitary individuals; a male traveling with 2 females moved 1,926–2,963 m in 24 h (Ammann 1985).

Communication.—*Rhinoceros sondaicus* is said to have poor eyesight but keen senses of smell and hearing, and it displays various types of audible sounds (Hazenwinkel 1933; Hoogerwerf 1970; Sody 1959; Talbot 1960). Ammann (1985) recorded 5 different vocalizations: “neigh,” the “loud blowing whistle” of Schenkel and Schenkel-Hulliger (1969b), not staccato like a horse and probably a contact call used over long distances; “bleat,” shorter than the bleat of sheep, a contact sound between female and young; “snort” like a steam engine, made separately or in series and a reaction to disturbances and used in an agonistic context, perhaps generally a threat; “shriek,” a very high pitch and probably a more intense form of snort, where fear is predominating; and “lip vibration” resembling the same sound in horses, perhaps a comfort behavior, made, for example, by a feeding individual. Roaring, perhaps from fighting individuals and loud enough to carry 800–1,000 m, was also described by Hoogerwerf (1970:80), who characterized it as “frightful ... resembling the trumpeting of an elephant or the furious low of a banteng bull” and “a terrible and ominous ‘woo-woo’ and later ‘wook’.” Various “low growls,” “savagely sniffing and snorting,” and “short, intermittent barks” of *R. sondaicus* were described by Hazewinkel (1933). Hoogerwerf (1970:80) believed that most audible sounds, such as loud sniffing, snorting, and puffing, have “without exception ... an unpleasant note to them and can often be heard over several hundred metres.” Other species of rhinoceroses emit relatively unique infrasounds (> 20 Hz, inaudible to humans), but *R. sondaicus* has not been studied for such sounds (von Muggenthaler et al. 1993).

Presumably a form of scent-marking, snorting marks of *R. sondaicus* are made by blowing secretions out of its nostrils; some have said that the liquid was clear when initially blown onto vegetation and turned with time to a reddish tint and finally a turbid orange color with a “penetrating odor”

(Hoogerwerf 1970:81; Sody 1959:215). Schenkel and Schenkel-Hulliger (1969a, 1969b) and Ammann (1985) made no mention of these snorting marks, and it may be that Hoogerwerf (1970) was mistaken as to their origin, and that urine squirting was the actual cause of the marks. Both female and male *R. sondaicus* ritualistically spray urine on vegetation, sometimes in copious amounts, particularly females in estrus (Hoogerwerf 1970), clearly invoking olfactory detection by conspecifics; apparently dominant males squirt urine much more than less dominant ones (Ammann 1985).

Early observations, before numbers of *R. sondaicus* were so strongly reduced, suggested that feces were deposited in piles (Sody 1959) perhaps to advertise one’s presence, similar to Indian rhinoceros (G. B. Schaller, pers. comm.), nilgai (*Boselaphus tragocamelus*—Leslie 2008), and four-horned antelope (*Tetracerus quadricornis*—Leslie and Sharma 2009) among others. Hoogerwerf (1970) and Schenkel and Schenkel-Hulliger (1969b) thought there was little evidence that remaining individuals intentionally defecate in the same spots, but Ammann (1985) found differently: 23% of all dung deposits were in piles; on 40% of occasions when an individual *R. sondaicus* encountered dung, it would defecate as well, and on 29% of occasions when groups encountered dung, they would do so (there was no difference between sexes). *R. sondaicus* may scrape a foot before defecation, but it does not actually kick its feces as do African species of rhinoceroses (Groves 1972; Hillman-Smith and Groves 1994). In general, 60% of dung piles are found in or next to water, and 22% on or next to trails (including those cut by humans—Ammann 1985).

Miscellaneous behavior.—*Rhinoceros sondaicus* is active at all times of day and night but frequently rests around noon during the heat of the day (Ammann 1985). Wet wallows are critically important in the habitat and behavioral repertoire of all Asian rhinoceroses (Ammann 1985; Blyth 1875; Groves and Kurt 1972; Hoogerwerf 1970; Laurie et al. 1983). *R. sondaicus* uses freshwater wallows in Ujung Kulon that are well concealed by jungle vegetation (Ammann 1985) and are relatively evenly spaced. Repeated use results in their persistence (Hoogerwerf 1970). Wallows in Ujung Kulon generally are 3–5 m wide, 6–7 m long, and 50 cm from the water’s surface to a mud layer 50–75 cm deep. In Ujung Kulon, Hoogerwerf (1970) contended that they occur “on low hills and ridges built up from marly soils and therefore with a high lime content” (Hoogerwerf 1970:115), but Ammann (1985) found them mostly in flat areas often associated with shade-providing and concealing *Arenga* palm (never bamboo). Multiple *R. sondaicus* may visit the same wallow, even together, and they frequently urinate in them to point that they can be “smelt dozens of metres away” by an odor “reminiscent of that of a large quantity of fresh horse dung” (Hoogerwerf 1970:115, plates 20–24). On the average, *R. sondaicus* wallows 0.7–0.8 times/24 h (Ammann 1985).



Fig. 7.—Typical stream and river (inset) habitats in Ujung National Park, West Java; *Rhinoceros sondaicus* often forages along the banks of such areas and uses them to wallow when those in the forest interior dry up. Photographs by C. P. Groves.

Wallows also can be detected by well-worn paths, muddy vegetation, and trees that have been repeatedly rubbed with the head and horns of departing rhinoceroses. The reasons for wallowing include thermoregulation, skin conditioning, avoidance or removal of ectoparasites, and olfactory advertisement by impregnating the skin with the urine-rich water of the wallow (Ammann 1985; Hoogerwerf 1970; Schenkel and Schenkel-Hulliger 1969a; Sody 1959). When such wallows dry up during drought, *R. sondaicus* frequents edges of muddy river banks and tidal forests (Fig. 7; see video at <http://www.arkive.org/javan-rhinoceros/rhinoceros-sondaicus/video-so08.html>, accessed 15 September 2010).

GENETICS

Chromosomal characteristics of *Rhinoceros sondaicus* have not been determined, but the diploid number ($2n$) of the congeneric Indian rhinoceros is 82 with no abnormal karyotypes noted to date (Houck 2001; Houck et al. 1995; Wurster and Benirschke 1968). Abnormal chromosomal complements in other species of rhinoceroses are suspected of compromising health and success of conservation efforts (Houck 2001; Houck et al. 1995).

Analyses of complete sequences of the mitochondrial 12S rRNA and cytochrome-*b* genes suggest that Asian and African rhinoceroses diverged about 26 million years ago and that the Sumatran rhinoceros forms a sister clade with the 2 species of *Rhinoceros* (Tougaard et al. 2001). Only 3

haplotypes have been identified in extant *R. sondaicus*: 2 in Java and 1 in Vietnam (Fernando et al. 2006). Evaluation of segments of the mitochondrial 12S rRNA gene extracted from feces showed that haplotypes of *R. sondaicus* from Java and Vietnam (0.5%) diverge to a similar extent as in subspecies of African rhinoceroses (0.5–0.9%) and confirmed the congeneric status of *R. sondaicus* and the Indian rhinoceros in the one-horned clade (Fernando et al. 2006). The same evaluation of segments of the D-loop (Fernando et al. 2006) showed that sequence divergence between *R. sondaicus* from Java and Vietnam was 4.8–5.1% compared to 7.2% for white rhinoceroses (*Ceratotherium simum*—Groves 1972) and 3.4–4.3% for black rhinoceroses (*Diceros bicornis*—Hillman-Smith and Groves 1994). Additional genetic studies are underway in Vietnam (Larson 2009).

Forensically, segments of the cytochrome-*b* gene, even from degraded samples (e.g., horn powder), can differentiate *R. sondaicus* from other species of rhinoceroses and mammals (Hsieh et al. 2003). Furthermore, Kimura's genetic distances from forensic analyses were 0.0539 between *R. sondaicus* and the Indian rhinoceros but 0.1147–0.1414 among *R. sondaicus* and all other species of rhinoceroses (Hsieh et al. 2003). Those disparities paralleled conventional phylogenies based on morphologic characteristics (Groves 1967, 1983; Grubb 2005) but not all molecular analyses (Tougaard et al. 2001). Along with genetic forensics (Hsieh et al. 2003), isotope analysis could be a valuable tool to differentiate confiscated horns and other tissues (Hall-Martin et al. 1993).

CONSERVATION

All 5 species of rhinoceroses are in need of ongoing, and in some cases, accelerated, conservation attention, with the 2 African species and the Indian rhinoceros doing better than the 2 southeastern Asian species that suffered to a greater extent from habitat loss to agriculture and poaching (e.g., Dinerstein 2003, 2011; Foose 1993; Stanley Price 1993). Not unlike the other species of rhinoceroses, the demise of *Rhinoceros sondaicus* beginning in the 1800s through the early 1900s was directly related to “activities of unscrupulous hunters and professional poachers” (Hoogerwerf 1970:51) and habitat degradation from agriculture activities in critical fertile lowland areas (Ramono et al. 1993), typically high in biodiversity (Dudgeon 2000). Poaching is a perennial threat to all species of rhinoceroses, particularly as the sophistication of the poachers has increased (Dinerstein 2011; Martin 1993). *R. sondaicus* is very vulnerable given its extremely low population levels (Schenkel and Schenkel-Hulliger 1969b; van Strien and Rookmaaker 2010)—indeed, perhaps the last *R. sondaicus* in Vietnam was poached in 2010 (Poston 2010).

Sadly, the market for body parts of rhinoceroses used in Arabian and Asian cultural and medical practices still

persists (Hoogerwerf 1954; Martin 1993). Horns have, in the past, been said to be an aphrodisiac, but this is a limited, and relatively unimportant, belief mainly in Gujarat, India. Horns also have been claimed to be a curative for snake bites and useful to identify poisonous drinks (Hoogerwerf 1970); for the latter belief, there may perhaps be some slight rationale because rhinoceros horn is fairly high in calcium that might react with certain poisons. The overwhelming threat is from the demand for rhinoceros horn as a fever-reducing drug in traditional Chinese medicine, and horns from Asian species command prices 10 times higher than African species (e.g., Taiwan—Hall-Martin et al. 1993). Evidence suggests there is no medical value in using rhinoceros horn in particular. Extract of rhinoceros horn in water reduced body temperature of laboratory rats (*Rattus norvegicus*) to a small extent, but so did horn extract of the domestic water buffalo (*Bubalus bubalis*—But et al. 1990) and the 2 critically endangered species of saiga (western saiga [*Saiga tatarica*] and Mongolian saiga [*S. monogolia*]—Groves and Leslie 2011; Sokolov 1974 [both recently under assault to feed gluttonous Chinese medicinal markets]). Horn from the domestic water buffalo is widely available, but the cultural perception of the superior medicinal value of rhinoceros horn is very difficult to overcome (But et al. 1990). Similarly, decoctions of 8 herbs (= Qingying Decoction) by themselves and with rhinoceros or water buffalo horn had about the same antipyretic effect (But et al. 1991). Stomach contents, ground teeth and hooves, blood, urine, and “salt” from the hide are believed to have “great medicinal values” in treating everything from leprosy to venereal diseases (Harper 1945; Hoogerwerf 1970:67; Sody 1959). Basically, no evidence exists to substantiate such uses, and ongoing conservation activities would benefit from the closure of these markets (Martin 1993), eliminating illegal harvest of *R. sondaicus* and other species of rhinoceroses.

Rhinoceros sondaicus is protected by many national and international regulations. It has been classified as “Critically Endangered” by the International Union for Conservation of Nature and Natural Resources since 1996 (van Strien et al. 2008), protected under Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (2010) since 1975, and listed as internationally Endangered by the United States Fish and Wildlife Service (1970) since 1970. For many years, numerous popular and semitechnical publications have decried the critically endangered status of *R. sondaicus* in southeastern Asia (e.g., Amin et al. 2006; Anonymous 1982; Blanford 1939; Dollman 1932, 1937; Hoogerwerf 1954; Page 1934; Pramono 1991; Raloff 1999; Ramono et al. 1993; Reynolds 1954; Sadjudin 1991; Santiapillai 1992; Schaurte 1968; Sriyanto and Haryono 1997). Nevertheless, scientific studies to elucidate the many aspects of its biology and ecology, which are fundamental for its survival and recovery, have been slow in coming. That,

limited funding, complexities of on-the-ground action (e.g., Polet and Ling 2004), and melding local, national, and international interests—a necessity (Ramono et al. 2009; Stanley Price 1993)—may have hampered action beyond critical steps to protect *R. sondaicus* from poaching and habitat destruction.

Some threats to *R. sondaicus* are beyond human influence. Ujung Kulon in West Java is vulnerable to volcanic and seismic activity. The major eruption of nearby Krakatoa in 1883 did not appear to diminish numbers of people or, apparently, *R. sondaicus* in Ujung Kulon, but 1 human settlement was abandoned 20 years later, likely the result of disease or problems with tigers (van Strien and Rookmaaker 2010 cf. Fernando et al. 2006). Absence of agricultural activities and forest thinning posteruption near that former settlement may have diminished habitat quality of *R. sondaicus* in localized areas. The devastating 2004 tsunami in the Indian Ocean did not negatively affect Ujung Kulon National Park or *R. sondaicus* (World Conservation Monitoring Centre 2005).

At a recent meeting of the Asian Rhino Specialist Group, conservation strategies to recover *R. sondaicus* were outlined yet again, but given the worldwide population of only about 50 individuals, the challenges are daunting (Talukdar et al. 2009). Genetic analyses have demonstrated that *R. sondaicus* from Java and Vietnam represent evolutionarily significant units (Fernando et al. 2006), which complicates bolstering the Vietnam population—probably no longer viable (van Strien et al. 2008) and perhaps extinct (Dinerstein 2011)—with individuals from Java. Proposals to establish another free-ranging population have been discussed for many years (Foose and van Strien 1997; Khan 1989; Ramono et al. 1993), but identification of suitable relocation sites has been problematic (Hariyadi et al. 2006; Ramono et al. 2009; Talukdar et al. 2009; van Merm 2008; van Strien et al. 2008) and removing individuals from a very small founder population provides little margin for error (Foose 1993). Under strict protection, the population in Ujung Kulon was able to increase by a minimum of 3 individuals and a maximum of 8 individuals in about 3 years, from 46–53 ($\bar{X} = 49.5$) in 1978 to 47–57 ($\bar{X} = 52$) in 1980 (Ammann 1985). Current plans involve establishing a 2nd population by relocating individuals from Ujung Kulon to nearby Javan islands (Dinerstein 2011). It may be unrealistic to bring back *R. sondaicus* to any semblance of normalcy, but aggressive contemporary conservation actions could be used to avoid extinction of this ancient species.

ACKNOWLEDGMENTS

The Rhino Resource Center maintains a remarkable Web site (<http://www.rhinoresourcecenter.com>), sponsored in part by the International Rhino Foundation (<http://www.rhinos-irf.org>), at which many references on all species of rhinoceroses are freely available electronically; these

resources were invaluable while preparing this monograph. We thank A. L. Gardner, United States Geological Survey, Patuxent Wildlife Research Center, for critical input on our synonymy; R. Sabin and K. Anderson, Natural History Museum (London), for assistance with the skull images; D. Wingreen-Mason, Cullman Collection, Smithsonian Libraries, Washington, D.C., and the entire staff of Interlibrary Loan Services, Oklahoma State University, for providing copies of seminal pages from rare literature; and G. B. Schaller, Wildlife Conservation Society and Panthera, J. A. Jenks, South Dakota State University, and E. Dinerstein, World Wildlife Fund, for their comments on earlier drafts of this monograph. The Oklahoma Cooperative Fish and Wildlife Research Unit (Oklahoma State University, Oklahoma Department of Wildlife Conservation, United States Geological Survey, United States Fish and Wildlife Service, and Wildlife Management Institute cooperating) provided technical support during the preparation of this monograph.

LITERATURE CITED

- AIMI, M., AND SUDIJONO. 1979. On the problematical species *Aceratherium boschi* von Koenigswald 1933. *Bulletin of the Geological Research and Development Centre* 1:37–45.
- ALI, S., AND H. SANTAPAU. 1958. Re-discovery of the smaller Asiatic onehorned rhinoceros (*Rhinoceros sondaicus* Desmarest) in Malaya. *Journal of the Bombay Natural History Society* 55:554–556.
- ALIKODRA, H. 1987. The ecology of the banteng (*Bos javanicus*) in the national park of Ujung Kulon. Pp. 161–166 in *Symposium on the Conservation and Management of Endangered Plants and Animals*. Special Publication 30. Southeast Asian Regional Centre for Tropical Biology, Bogor, Indonesia.
- AMIN, R., K. THOMAS, R. H. EMSLIE, T. J. FOSSE, AND N. VAN STRIEN. 2006. An overview of the conservation status of and threats to rhinoceros species in the wild. *International Zoo Yearbook* 40: 96–117.
- AMMANN, H. 1985. Contributions to the ecology and sociology of the Javan rhinoceros (*Rhinoceros sondaicus* Desm.). Inaugural dissertation, Universität Basel, Basel, Switzerland.
- ANASTOS, G. 1950. The scutate ticks, or Ixodidae, of Indonesia. *Entomologica Americana* 30:1–144.
- ANONYMOUS. 1874. On the new rhinoceros at the Zoological Gardens. *Nature* 9(12):363–364.
- ANONYMOUS. 1982. What future for Javan rhinos? *Oryx* 16:393–394.
- ANSELL, W. F. H. 1947. A note on the position of *Rhinoceros* in Burma. *Journal of the Bombay Natural History Society* 47:249–278.
- ASHBY, K. R., AND C. SANTIAPILLAI. 1988. The status of the banteng (*Bos javanicus*) in Java and Bali. *Tigerpaper* 15(4):16–25.
- BACON, A.-M., ET AL. 2004. The Pleistocene Ma U’Oi cave, northern Vietnam: paleontology, sedimentary and palaeoenvironments. *Geobios* 37:305–314.
- BARBOUR, T., AND G. M. ALLEN. 1932. The lesser one-horned rhinoceros. *Journal of Mammalogy* 13:144–149.
- BARNARD, B. F. H. 1932. The one-horned rhinoceros. *Malayan Forester* 1:183–185.
- BEDDARD, F. E. 1889. On the anatomy of *Rhinoceros sumatrensis*. *Proceedings of the Zoological Society of London* 1889:7–25.
- BEDDARD, F. E., AND F. TREVES. 1887. On the anatomy of the Sondaic rhinoceros. *Transactions of the Zoological Society of London* 12: 183–197.
- BEDEN, M., AND C. GUÉRIN. 1973. Le gisement de vertébrés du Phnom Loang (Province de Kampot, Cambodge). Faune Pléistocène moyen terminal (Loangien). *Travaux et Documents de l’Office de la Recherche Scientifique et Technique d’Outre-Mer (Paris)* 75: 6–97.
- BEQUAERT, J. 1933. The giant ticks of the Malayan rhinoceroses; with a note on *Ixodes walckenaerii* Gervais. *Psyche* 1933:137–143.
- BLANFORD, H. R. 1939. *Rhinoceros sondaicus* in Burma: the problem of conservation. *Journal of the Society for the Preservation of the Fauna of the Empire, New Series* 37:27–32.
- BLOUCH, R. A. 1988. Ecology and conservation of the Javan warty pig *Sus verrucosus* Müller, 1840. *Biological Conservation* 43:295–307.
- BLYTH, E. 1862. A memoir of the living Asiatic species of rhinoceros. *Journal of Asiatic Society of Bengal* 31:151–175.
- BLYTH, E. 1875. Catalogue of mammals and birds of Burma, by the late E. Blyth. *Journal of Asiatic Society of Bengal* 44(2, extra issue): 1–167.
- BONTIUS, J. 1658. *Historiæ naturalis & medicæ. Liber quintus, de quadrupedibus, avibus, & piscibus. Caput I, de Abada, siue Rhinocerote*. Pp. 50–52 in *De Indiæ utriusque re naturali et medica, libri quatuordecim, quorum contenta pagina sequens exhibit* (G. Piso, ed.). Apud Ludovicum et Danielem Elzevirios, Amsterdam, The Netherlands.
- BRANDON-JONES, C. 1997. Edward Blyth, Charles Darwin, and the animal trade in nineteenth-century India and Britain. *Journal of the History of Biology* 30:145–178.
- BURTON, R. W. 1951. Game sanctuaries in Burma (pre-1942) with present status of rhinoceros and thamin. *Journal of the Bombay Natural History Society* 49:729–737.
- BUT, P. P.-H., L.-C. LUNG, AND Y.-K. TAM. 1990. Ethnopharmacology of rhinoceros horn. I: antipyretic effects of rhinoceros horn and other animal horns. *Journal of Ethnopharmacology* 30:157–168.
- BUT, P. P.-H., Y.-K. TAM, AND L.-C. LUNG. 1991. Ethnopharmacology of rhinoceros horn. II: antipyretic effects of prescriptions containing rhinoceros horn or water buffalo horn. *Journal of Ethnopharmacology* 33:45–50.
- CARTER, T. D., AND J. E. HILL. 1942. Notes on the lesser one-horned rhinoceros, *Rhinoceros sondaicus*. 1, a skull of *Rhinoceros sondaicus* in the American Museum of Natural History. *American Museum Novitates* 1206:1–3.
- CAVE, A. J. E. 1965. Traction epiphyses in the mammalian skull. *Proceedings of the Zoological Society of London* 145:495–508.
- CAVE, A. J. E. 1969. Hairs and vibrissae in the Rhinocerotidae. *Journal of Zoology (London)* 157:247–257.
- CAVE, A. J. E. 1985. An unrecorded specimen of the Javan rhinoceros (*Rhinoceros sondaicus*). *Journal of Zoology (London)* 207: 527–535.
- CAVE, A. J. E., AND F. J. AUMONIER. 1963. The visceral histology of the Sumatran rhinoceros. *Journal of the Royal Microscopical Society* 82:29–37.
- CERDEÑO, E. 1995. Cladistic analysis of the family Rhinocerotidae (Perissodactyla). *American Museum Novitates* 3143:1–25.
- CHAUHAN, P. R. 2008. Large mammal fossil occurrences and associated archaeological evidence in Pleistocene contexts of peninsular India and Sri Lanka. *Quaternary International* 192:20–42.
- CLARKE, T. H. 1986. *The rhinoceros from Dürer to Stubbs, 1515–1799*. Sotheby’s Publications, London, United Kingdom.
- COLBERT, E. H. 1942. Notes on the lesser one-horned rhinoceros, *Rhinoceros sondaicus*. 2. The position of *Rhinoceros sondaicus* in the phylogeny of the genus *Rhinoceros*. *American Museum Novitates* 1207:1–6.
- COLE, F. J. 1953. The history of Albrecht Dürer’s rhinoceros in zoological literature. Pp. 337–356 in *Science, medicine, and history: essays on the evolution of scientific thought and medical practice written in honour of Charles Singer* (E. A. Underwood, ed.). Oxford University Press, Oxford, United Kingdom.
- COMYN-PLATT, T. 1937. A report on fauna preservation in Malaya. *Journal of the Society for the Preservation of the Fauna of the Empire* 30:45–52.
- CONVENTION ON INTERNATIONAL TRADE IN ENDANGERED SPECIES OF WILD FAUNA AND FLORA. 2010. Appendices I. www.cites.org/eng/app/appendices.shtml, accessed 14 February 2010.
- CORBET, G. B., AND J. E. HILL. 1992. *The mammals of the Indomalayan region: a systematic review*. Oxford University Press, Oxford, United Kingdom.
- CRANBROOK, EARL OF. 1986. A review of fossil and prehistoric remains of rhinoceroses of Borneo. *Sabah Museum and Archives Journal* 1:50–110.

- CRANBROOK, EARL OF, AND P. J. PIPER. 2007. The Javan rhinoceros *Rhinoceros sondaicus* in Borneo. *The Raffles Bulletin of Zoology* 55:217–220.
- CUVIER, G. 1829. Le règne animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Nouvelle édition, Revue et augmentée, tome 1. Chez Déterville, Libraire, et Chez Crochard, Libraire, Paris, France.
- DALTRY, J. C., AND F. MOMBERG. 2000. Cardamom Mountains: biodiversity survey 2000. Fauna & Flora International, Cambridge, United Kingdom.
- DAMMERMAN, K. W. 1934. On prehistoric mammals from the Sampoeng Cave, Central Java. *Treubia* 14:477–486.
- DE BEAUFORT, L. F. 1928. On the occurrence of *Rhinoceros sondaicus* Desm. in Sumatra. *Tijdschrift der Nederlandsche Dierkundige Vereeniging, Series 3* 1:43–44.
- DE LONGH, H. H., H. H. T. PRINS, N. J. VAN STRIEN, AND L. C. ROOKMAAKER. 2005. Some observations on the presence of one-horned rhinos in the bas reliefs of the Angkor Wat Temple Complex, Cambodia. *Pachyderm* 38:98–100.
- DE PONCINS, V. E. 1935. A hunting trip in the Sunderbunds in 1892. *Journal of the Bombay Natural History Society* 37:844–858.
- DERANIYAGALA, P. E. P. 1937. Some Miocene and Upper Siwalik vertebrates from Ceylon. *Ceylon Journal of Science B* 10:191–200.
- DERANIYAGALA, P. E. P. 1938. Some fossils from Ceylon. Part II. *Journal of the Ceylon Branch of the Royal Asiatic Society of Great Britain and Ireland* 34:231–239.
- DERANIYAGALA, P. E. P. 1946. Some mammals of the extinct Ratnapura fauna of Ceylon. *Spolia Zeylanica* 24:161–167.
- DESMAREST, A. G. 1822. Mammalogie ou description de espèces de mammifères. Seconde partie, contenant les orders des rongeurs, des édentés, des pachyderms, des ruminans et des cétacés. Chez Mme. Veuve Agasse, Imprimeur-Libraire, Paris, France. [Two parts paginated sequentially: Première partie, pages 1–276, dated 1820, and Seconde partie, dated 1822, pages 277–555; presented as a single volume online at www.archive.org, accessed 24 July 2009.]
- DINERSTEIN, E. 1991. Seed dispersal by the greater one-horned rhinoceros (*Rhinoceros unicornis*) and the flora of rhinoceros latrines. *Mammalia* 55:355–362.
- DINERSTEIN, E. 1992. Effects of *Rhinoceros unicornis* on riverine forest structure in lowland Nepal. *Ecology* 73:701–704.
- DINERSTEIN, E. 2003. Return of the unicorns: the natural history and conservation of the greater one-horned rhinoceros. Columbia University Press, New York.
- DINERSTEIN, E. 2011. Family Rhinocerotidae. Pp. 144–181 in *Handbook of the mammals of the world*. Vol. 2. Hoofed mammals (D. E. Wilson and R. A. Mittermeier, eds.). Lynx Edicions, Barcelona, Spain.
- DINERSTEIN, E., AND C. M. WEMMER. 1988. Fruits rhinoceroses eat: dispersal of *Trewia nudiflora* (Euphorbiaceae) in lowland Nepal. *Ecology* 69:1168–1174.
- DOLLMAN, J. G. 1932. The Javan rhinoceros. *Natural History Magazine* 3:273–277.
- DOLLMAN, J. G. 1937. Mammals which have recently become extinct in British North Borneo. *Journal of the Society for the Preservation of the Fauna of the Empire* 30:67–74.
- DOVER, C. 1932. The duration of life of some Indian animals. *Indian Forester* 58:81–90.
- DUBOIS, E. 1908. Das Geologische Alter der Kendeng oder Trinil-Fauna. *Tijdschrift van de Koninklijke Vereeniging voor Nederlandse Aardrijkskunde, Series 2* 25:1235–1270.
- DUDGEON, D. 2000. Large-scale hydrological changes in tropical Asia: prospects for riverine biodiversity. *BioScience* 50:793–806.
- DUNCAN, F. M. 1937. On the dates of publications of the Society's 'Proceedings,' 1859–1926. With an appendix containing the dates of publication of 'Proceedings,' 1830–1858, compiled by the late F. H. Waterhouse, and of the 'Transactions,' by the late Henry Peavot, originally published in P.Z.S. 1893, 1913. *Proceedings of the Zoological Society of London, A. General and Experimental* 107: 71–84.
- ELLIOT, H. S. R., AND A. G. THACKER (TRANSLATORS). 1911. *Beast and men: being Carl Hagenbeck's experiences for half a century among wild animals*. An abridged translation, Longmans, Green, and Company, London, United Kingdom.
- EVANS, G. H. 1905. Notes on rhinoceroses in Burma, *R. sondaicus* and *sumatrensis*. *Journal of the Bombay Natural History Society* 16: 555–561.
- FALCONER, H., AND P. T. CAUTLEY. 1847. *Fauna antiqua sivalensis*. Part VIII. Suidae and Rhinocerotidae. Smith Elder, London, United Kingdom.
- FERNANDO, P., G. POLET, N. FOEAD, L. S. NG, J. PASTORINI, AND D. J. MELNICK. 2006. Genetic diversity, phylogeny and conservation of the Javan rhinoceros (*Rhinoceros sondaicus*). *Conservation Genetics* 7:439–448.
- FETHERSTONHAUGH, A. H. 1951. Rhinoceroses. *Malayan Nature Journal* 5:191–193.
- FINLAYSON, H. H. 1950. Note on the cranial and dental characters of a specimen of *Rhinoceros sondaicus* Desm. *Proceedings of the Zoological Society of London* 120:151–154.
- FLOWER, S. S. 1900. On the Mammalia of Siam and the Malay Peninsula. *Proceedings of the Zoological Society of London* 1900: 306–379.
- FOOSE, T. J. 1993. Global management of rhinos. Pp. 32–47 in *Proceedings of an international conference: rhinoceros biology and conservation* (O. A. Ryder, ed.). Zoological Society of San Diego, San Diego, California.
- FOOSE, T. J., AND N. J. VAN STRIEN. 1995. Javan rhino stamp. *Asian Rhinos* 1:15.
- FOOSE, T. J., AND N. VAN STRIEN (EDS). 1997. Asian rhinos: status survey and conservation action plan. Asian Rhino Specialist Group, International Union Conservation of Nature and Natural Resources, Gland, Switzerland.
- FRASER, O. L. 1875. Note on a partially ossified nasal septum in *Rhinoceros sondaicus*. *Journal of the Asiatic Society of Bengal* 44: 10–12.
- FRECHKOP, S. 1951. Notes sur les mammifères. 38—sur un foetus de rhinoceros de la Sonde. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique* 27:1–7.
- GARROD, A. H. 1877a. On some points in the visceral anatomy of the rhinoceros of the Sunderbunds (*Rhinoceros sondaicus*). *Proceedings of the Zoological Society of London* 1877:707–711.
- GARROD, A. H. 1877b. On the *Tania* of the rhinoceros of the Sunderbunds (*Plagiotaenia gigantea*, Peters). *Proceedings of the Zoological Society of London* 1877:788–789.
- GEOFFROY SAINT-HILAIRE, É., AND F. CUVIER. 1824. Unnumbered page associated with pl. 309, vol. vi, livr. 45 in *Histoire naturelle des mammifères, avec figures originales, coloriées, dessinées d'après des animaux vivants; publiée sous l'autorité de l'Administration du Muséum d'Histoire Naturelle*. Tome cinquième. Chez A. Belin, Libraire-Éditeur, Paris, France.
- GRAY, J. E. 1868. Observations on the preserved specimens and skeletons of the Rhinocerotidae in the collection of the British Museum and Royal College of Surgeons, including the descriptions of three new species. *Proceedings of Zoological Society of London* 1867:1003–1032. [Dated 1867 but published April 1868 according to Duncan 1937.]
- GRIFFITH, E., C. HAMILTON-SMITH, AND E. PIDGEON (EDS). 1827. The animal kingdom, arranged in conformity with its organization, by the Baron Cuvier, with additional descriptions of all the species hitherto named, and of many not before noticed. Vol. V. Synopsis of the species of the class Mammalia, as arranged with reference to their organization. G. B. Whittaker, London, United Kingdom.
- GROVES, C. P. 1967. On the rhinoceroses of south-east Asia. *Säugetierkundliche Mitteilungen* 15:221–237.
- GROVES, C. P. 1971. Species characters in rhinoceros horns. *Zeitschrift für Säugetierkunde* 36:238–252.
- GROVES, C. P. 1972. *Ceratotherium simum*. *Mammalian Species* 8:1–6.
- GROVES, C. P. 1982a. Asian rhinoceroses: down but not out. *Malayan Naturalist* 36:11–22.
- GROVES, C. P. 1982b. The skulls of Asian rhinoceroses: wild and captive. *Zoo Biology* 1:251–261.
- GROVES, C. P. 1983. Phylogeny of the living species of rhinoceros. *Zeitschrift für Zoologische Systematik und Evolutionsforschung* 21:293–313.
- GROVES, C. P. 1993. Testing rhinoceros subspecies by multivariate analysis. Pp. 92–100 in *Proceedings of an international conference:*

- rhinoceros biology and conservation (O. A. Ryder, ed.). Zoological Society of San Diego, San Diego, California.
- GROVES, C. P. 1995a. Why the Cat Loc (Vietnam) rhinos are Javan. *Asian Rhinos* 2:8–9.
- GROVES, C. P. 1995b. A comment on Haryono et al.'s report. *Asian Rhinos* 2:9.
- GROVES, C. P., AND S. CHAKRABORTY. 1983. The Calcutta collection of Asian rhinoceros. *Records of the Zoological Survey of India* 80: 251–263.
- GROVES, C. P., AND C. GUÉRIN. 1980. Le *Rhinoceros sondaicus annamiticus* (Mammalia, Perissodactyla) d'Indochine: distinction taxinomique et anatomique; relations phyletiques. *Géobios* 13: 199–208.
- GROVES, C. P., AND F. KURT. 1972. *Dicerorhinus sumatrensis*. *Mammalian Species* 21:1–6.
- GROVES, C. P., AND D. M. LESLIE, JR. 2011. Family Bovidae. Pp. 444–572 in *Handbook of the mammals of the world*. Vol. 2. Hoofed mammals (D. E. Wilson and R. A. Mittermeier, eds.). Lynx Edicions, Barcelona, Spain.
- GRUBB, P. 2005. Order Perissodactyla. Pp. 629–636 in *Mammal species of the world: a taxonomic and geographic reference* (D. E. Wilson and D. M. Reeder, eds.). 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.
- GUÉRIN, C., AND C. MOURER. 1969. Le *Rhinoceros sondaicus* Desmarest du gisement neolithique de Loang Spean, province de Battambang, Cambodge. *Documents des Laboratoires de Geologie de la Faculte des Sciences Lyon* 31:39–53.
- HALL-MARTIN, A. J., ET AL. 1993. Determination of species and geographic origin of rhinoceros horns by isotopic analysis and its possible application to trade control. Pp. 123–135 in *Proceedings of an international conference: rhinoceros biology and conservation* (O. A. Ryder, ed.). Zoological Society of San Diego, San Diego, California.
- HARIYADI, A. R., ET AL. 2006. Halimun-Salak National Park as a potential site for establishing the second population of Javan rhinoceros (*Rhinoceros sondaicus*). *World Wildlife Fund*, Bogor, Indonesia.
- HARPER, F. 1945. Extinct and vanishing mammals of the Old World. Special Publication 12. American Committee for International Wild Life Protection, New York Zoological Park, New York 12:1–850.
- HAYSSEN, V., A. VAN TIENHOVEN, AND A. VAN TIENHOVEN. 1993. Asdell's patterns of mammalian reproduction: a compendium of species-specific data. Cornell University Press, Ithaca, New York.
- HAZEWINKEL, J. C. 1933. *Rhinoceros sondaicus* in Zuid Sumatra. *Tropische Natuur* 22:101–109.
- HEISSIG, K. 1972. Paläontologische und geologische Untersuchungen im Tertiär von Pakistan. 5. Rhinocerotidae (Mamm.) aus den unteren und mittleren Siwalik-Schichten. *Abhandlungen der Bayerische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Neue Folge* 152:1–112.
- HEUDE, P. M. 1892. Étude sur les suillens. Chapitre II. Mémoires Concernant l'Histoire Naturelle de l'Empire Chinois par des Pères de la Compagnie de Jesus 2:85–115 + plates XIX–XXIX.
- HIGGINS, J. C. 1935. The game birds and animals of the Manipur State with notes of their numbers, migration and habits. *Journal of the Bombay Natural History Society* 37:298–309.
- HILLMAN-SMITH, A. K. K., AND C. P. GROVES. 1994. *Diceros bicornis*. *Mammalian Species* 455:1–8.
- HOAGE, R. J., A. ROSKELL, AND J. MANSOUR. 1996. Menageries and zoos to 1900. Pp. 8–18 in *New world, new animals: from menagerie to zoological park in the nineteenth century* (R. J. Hoage and W. A. Deiss, eds.). Johns Hopkins University Press, Baltimore, Maryland.
- HOGERWERF, A. 1954. Nature protection in Indonesia. *Oryx* 2: 220–227.
- HOGERWERF, A. 1970. Ujung Kulon: the land of the last Javan rhinoceros. E. J. Brill, Leiden, The Netherlands.
- HOOIJER, D. A. 1946a. The evolution of the skeleton of *Rhinoceros sondaicus* Desmarest. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* 49:671–676.
- HOOIJER, D. A. 1946b. Prehistoric and fossil rhinoceroses from the Malay Archipelago and India. *Zoologische Mededelingen*, Leiden 26:1–138.
- HOOIJER, D. A. 1948. *Rhinoceros sondaicus* Desmarest from Kitchen-Middens of Bindjai Tamiang, North Sumatra. *Geologie en Mijnbouw Nieuwe Serie* 10:116–117.
- HOOIJER, D. A. 1949. Mammalian evolution in the Quaternary of southern and eastern Asia. *Evolution* 3:125–128.
- HOOIJER, D. A. 1962a. Report on the collection of Pleistocene mammals from tin-bearing deposits in a limestone cave near Ipoh, Kinta Valley, Perak. *Federation Museum Journal* 7:1–5.
- HOOIJER, D. A. 1962b. *Rhinoceros sondaicus* Desmarest from the Hoabhinian of Gua Cha rock shelter, Kelantan. *Federation Museum Journal* 7:23–24.
- HOOIJER, D. A. 1964. New records of mammals from the Middle Pleistocene of Sangiran, Central Java. *Zoologische Mededelingen*, Leiden 40:73–87.
- HORSFIELD, T. 1824. *Zoological researches in Java, and the neighbouring islands*. Kingsbury, Parbury, & Allen, London, United Kingdom.
- HOUCK, M. L. 2001. Application of cytogenetics to conservation management of rhinoceroses. Pp. 51–53 in *The 1st international symposium on assisted reproductive technology for the conservation and genetic management of wildlife*. Henry Doorly Zoo, Omaha, Nebraska.
- HOUCK, M. L., O. A. RYDER, A. T. KUMAMOTO, AND K. BENIRSCHKE. 1995. Cytogenetics of Rhinocerotidae. *Internationalen Symposiums über der Erkrankungen Zootiere* 37:25–32.
- HSIEH, H.-M., ET AL. 2003. Species identification of rhinoceros horns using the cytochrome *b* gene. *Forensic Science International* 136: 1–11.
- JARDINE, W. 1836. *The naturalist's library*. Vol. XXIII. Mammalia. Thick-skinned quadrupeds. Henry G. Bohn, London, United Kingdom.
- JONES, D. M. 1979. The husbandry and veterinary care of captive rhinoceroses. *International Zoo Yearbook* 19:239–252.
- JONES, M. L. 1993. Longevity of ungulates in captivity. *International Zoo Yearbook* 32:159–162.
- KHAN, M (COMP.). 1989. Asian rhinos: an action plan for their conservation. Species Survival Commission Asian Rhino Specialist Group, International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.
- LARSON, R. 2009. Study planned for Javan rhinos in Vietnam. *International Zoo News* 56:420.
- LAURIE, W. A., E. M. LANG, AND C. P. GROVES. 1983. *Rhinoceros unicornis*. *Mammalian Species* 211:1–6.
- LESLIE, D. M., JR. 2008. *Boselaphus tragocamelus* (Artiodactyla: Bovidae). *Mammalian Species* 813:1–16.
- LESLIE, D. M., JR. 2011. Banteng *Bos javanicus*. P. 574 in *Handbook of the mammals of the world*. Vol. 2. Hoofed mammals (D. E. Wilson and R. A. Mittermeier, eds.). Lynx Edicions, Barcelona, Spain.
- LESLIE, D. M., JR., AND K. SHARMA. 2009. *Tetracerus quadricornis* (Artiodactyla: Bovidae). *Mammalian Species* 843:1–11.
- LESSON, R. P. 1838. *Complément de Buffon*. Deuxieme edition. Races humaines et mammifères. P. Pourrat Frères, Éditeurs, Paris, France.
- LOCH, C. H. 1937. *Rhinoceros sondaicus*. The Javan or lesser one-horned rhinoceros and its geographical distribution. *Journal of the Malayan Branch of the Royal Asiatic Society*, Singapore 15: 130–149.
- LYDEKKER, R. 1877. Descriptions of the molar teeth and other remains of Mammalia. *Memoirs of the Geological Survey of India, Paleontologia Indica* 10(1, 2):19–69 + plates iv–x.
- LYDEKKER, R. 1886a. The fauna of the Karnul Caves. *Memoirs of the Geological Survey of India, Palaeontologia Indica, Series X, Indian Tertiary & Post-Tertiary Vertebrata 4 Part II:22–58 + plates VII–XI*.
- LYDEKKER, R. 1886b. Preliminary note on the Mammalia of the Karnul Caves. *Records of the Geological Survey of India* 19:120–122.
- LYDEKKER, R. 1907. *The game animals of India, Burma, Malaya, and Tibet, being a new and revised edition of 'The great and small game of India, Burma, and Tibet.'* Rowland Ward, Limited, London, United Kingdom.
- LYDEKKER, R. 1916. *Catalogue of the ungulate mammals in the British Museum (Natural History)*. Vol. V. Perissodactyla (horses, tapirs,

- rhinoceroses), Hyracoidea (hyraxes), Proboscidae (elephants). Trustees of the British Museum, London, United Kingdom.
- MACKINNON, K., AND C. SANTIAPILLAI. 1991. Javan rhino: captive breeding concern. *Oryx* 25:65.
- MANAMENDRA-ARACHCHI, K., R. PETHIYAGODA, R. DISSANAYAKE, AND M. MEEGASKUMBURA. 2005. A second extinct big cat from the late Quaternary of Sri Lanka. *The Raffles Bulletin of Zoology*, Supplement 12:423–434.
- MANH, H. N. 2009. The status of vulnerable gaur *Bos gaurus* and endangered banteng *Bos javanicus* in Ea So Nature Reserve and Yok Don and Cat Tien national parks, Vietnam. *Oryx* 43: 129–135.
- MARTIN, E. B. 1993. The present-day trade routes and markets for rhinoceros products. Pp. 1–9 in *Proceedings of an international conference: rhinoceros biology and conservation* (O. A. Ryder, ed.). Zoological Society of San Diego, San Diego, California.
- MASON, F. 1882. *Burma, its people and productions; or, notes on the fauna, flora and minerals of Tenasserim, Pegu and Burma*. Vol. I. Geology, mineralogy and zoology. Rewritten and enlarged by W. Theobald. Stephen Austin & Sons, Hertford, United Kingdom.
- MAXWELL, G. 1907. In *Malay forests*. William Blackwood and Sons, Edinburgh, United Kingdom.
- MAZAK, V. 1981. *Panthera tigris*. *Mammalian Species* 152:1–8.
- MCNEELY, J. A., AND F. W. CRONIN. 1972. Rhinos in Thailand. *Oryx* 11:457–460.
- MCNEELY, J. A., AND A. LAURIE. 1977. Rhinos in Thailand. *Oryx* 13: 486–489.
- MILLER, G. S., JR. 1942. Zoological results of the George Vanderbilt Sumatran Expedition 1936–1939. Part V. Mammals collected by Frederick A. Ulmer Jr. on Sumatra and Nias. *Proceedings of the Academy of Natural Sciences* 94:107–165.
- MILTON, O., AND R. D. ESTES. 1963. *Burma wildlife survey, 1959–1960*. American Committee for International Wild Life Protection Special Publication 16, New York.
- MORRIS, R. C. 1935. To Malaya for a rhinoceros. *Journal of the Bombay Natural History Society* 38:438–446.
- MURPHY, D. 2004. The status and conservation of Javan rhinoceros, Siamese crocodile, Phasianidae and gaur in Cat Tien National Park, Vietnam. Cat Tien National Park Conservation Project, Technical Report 50:1–28.
- NEUVILLE, H. 1927. Remarques et comparaisons relatives aux phaneres des rhinoceros. *Archives du Muséum National d'Historie Naturelle de Paris*, Series 6 2:179–208.
- PAGE, R. 1934. Wild life in Malaya. *Journal of the Society for the Preservation of the Fauna of the Empire* 23:34–37.
- PALMIERI, J. R., PURNOMO, AND H. AMMAUN. 1980. Parasites of the lesser one-horned rhinoceros (*Rhinoceros sondaicus* Desmarest). *Journal of Parasitology* 66:1031.
- PEACOCK, E. H. 1933. *A game book for Burma and adjoining territories*. H. F. & G. Witherby, London, United Kingdom.
- PEDRONO, M., M. T. HA, P. CHOTEAU, AND F. VALLEJO. 2009. Status and distribution of the endangered banteng *Bos javanicus birmanicus* in Vietnam: a conservation strategy. *Oryx* 43:618–625.
- PETERS, W. 1878. Über *Rhinoceros inermis* Lesson. *Monatsberichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin*, 19 Februar 1977. *Sitzungsberichte der physikalisch-mathematischen Klasse* 1878:68–71.
- POCOCK, R. I. 1944. The premaxillae in the Asiatic rhinoceroses. *Annals and Magazine of Natural History*, Series 11, 11:834–842.
- POCOCK, R. I. 1945a. The nasal septum in existing Asiatic rhinoceroses. *Annals and Magazine of Natural History*, Series 11, 12:341–344.
- POCOCK, R. I. 1945b. Some cranial and dental characters of the existing species of rhinoceroses. *Proceedings of the Zoological Society of London* 114:437–450.
- POLET, G., AND S. LING. 2004. Protecting mammal diversity: opportunities and constraints for pragmatic conservation management in Cat Tien National Park, Vietnam. *Oryx* 38:186–196.
- POLETI, G., T. VAN MUI, N. X. DANG, B. H. MANH, AND M. BALTZER. 1999. The Javan rhinos, *Rhinoceros sondaicus annamiticus*, of Cat Tien National Park, Vietnam: current status and management implications. *Pachyderm* 27:34–48.
- POOLE, C. M., AND J. W. DUCKWORTH. 2005. A documented 20th century record of Javan rhinoceros *Rhinoceros sondaicus* from Cambodia. *Mammalia* 69:443–444.
- POSTON, L. 2010. Javan rhino found dead in Vietnam. World Wildlife Fund press release, Washington, D.C. www.worldwildlife.org, accessed 25 March 2011.
- PRAMONO, A. H. 1991. Determining the fate of the Javan rhino. *Voice of Nature* 93:16–17.
- PRATIKNYO, H. 1991. The diet of the Javan rhino. *Voice of Nature* 93: 12–13.
- PROTHERO, D. R. 1993. Fifty million years of rhinoceros evolution. Pp. 82–81 in *Proceedings of an international conference: rhinoceros biology and conservation* (O. A. Ryder, ed.). Zoological Society of San Diego, San Diego, California.
- PROTHERO, D. R., E. MANNING, AND C. B. HANSON. 1986. The phylogeny of the Rhinocerotidae (Mammalia, Perissodactyla). *Zoological Journal of the Linnean Society* 87:341–366.
- PUDYATMOKO, S., DJUWANTOKO, AND Y. SABARNO. 2007. Evidence of banteng (*Bos javanicus*) decline in Baluran National Park, Indonesia. *Journal of Biological Sciences* 7:854–859.
- PUTRO, H. R. 1997. Heterogenitas habitat badak Jawa (*Rhinoceros sondaicus* Desm. 1822) di Taman Nasional Ujung Kulon. *Media Konservasi Edisi Khusus 1997*:17–40.
- RALOFF, J. 1999. Rarest of the rare: remote-camera images and dung-heap data give a portrait of Vietnam's rhinos. *Science News* 156(10):153–155.
- RAMONO, W. S., C. SANTIAPILLAI, AND K. MACKINNON. 1993. Conservation and management of Javan rhino (*Rhinoceros sondaicus*) in Indonesia. Pp. 265–273 in *Rhinoceros biology and conservation: proceedings of an international conference* (O. A. Ryder, ed.). San Diego, Zoological Society, San Diego, California.
- RAMONO, W. S., ET AL. 2009. Report on a second habitat assessment for the Javan rhinoceros (*Rhinoceros sondaicus sondaicus*) within the island of Java. International Rhino Foundation, Yulee, Florida.
- REYNOLDS, E. A. P. 1954. Burma rhino. *Burmese Forester* 4:104–108.
- REYNOLDS, R. J. 1960. Asian rhinos in captivity. *International Zoo Yearbook* 2:17–42.
- REYNOLDS, R. J. 1961. Javan rhino in the Berlin Zoo. *International Zoo News* 8:76–77.
- RINALDI, D., Y. A. MULYANI, AND H. ARIEF. 1997. Status populasi dan perilaku badak Jawa (*Rhinoceros sondaicus* Desmarest) di TN Ujung Kulon. *Media Konservasi* 1997:41–47.
- ROOKMAAKER, L. C. 1980. Distribution of the rhinoceros in eastern India, Bangladesh, China, and the Indo-Chinese region. *Zoologischer Anzeiger* 205:253–268.
- ROOKMAAKER, L. C. 1982. The type locality of the Javan rhinoceros (*Rhinoceros sondaicus* Desmarest, 1822). *Zeitschrift für Säugetierkunde* 6:381–382.
- ROOKMAAKER, L. C. 1988. The Indo-Chinese rhinoceros. *Oryx* 22:241.
- ROOKMAAKER, L. C. 1993. The mysterious "Liverpool Rhinoceros." *Der Zoologische Garten Neue Folge* 63:246–258.
- ROOKMAAKER, L. C. 1997. Records of the Sundarbans rhinoceros (*Rhinoceros sondaicus inermis*) in India and Bangladesh. *Pachyderm* 24:37–45.
- ROOKMAAKER, L. C. 1998. The rhinoceros in captivity: a list of 2439 rhinoceroses kept from Roman times to 1994. Kugler Publications and SPB Academic Publishing, The Hague, The Netherlands.
- ROOKMAAKER, L. C. 2005. A Javan rhinoceros, *Rhinoceros sondaicus*, in Bali in 1839. *Zoologische Garten Neue Folge* 75:129–131.
- ROOKMAAKER, L. C. 2006. The demise of the lesser Indian rhinoceros. *Souvenir of Kaziranga Elephant Festival 2006*, Airawat 4:27–28.
- ROOKMAAKER, L. C., AND R. P. W. VISSER. 1982. Petrus Camper's study of the Javan rhinoceros (*Rhinoceros sondaicus*) and its influence on Georges Cuvier. *Bijdragen tot de Dierkunde, Amsterdam* 52: 121–136.
- SADJUDIN, H. R. 1984. Studi prilaku dan populasi badak Jawa (*Rhinoceros sondaicus* Desmarest, 1822) di Taman Nasional Ujung Kulon. *Skripsi Fakultas Biologi Universitas Nasional, Jakarta, Indonesia*. (not seen, cited in Ramono et al. 2009).
- SADJUDIN, H. R. 1987. The Javan rhino (*Rhinoceros sondaicus* Desm.) census in Ujung Kulon National Park. *Rimba Indonesia* 21:16–26.
- SADJUDIN, H. R. 1991. The misunderstood one-horned rhino. *Voice of Nature* 93:14–15.

- SANDGROUND, J. H. 1933. Two new helminths from *Rhinoceros sondaicus*. *Journal of Parasitology* 19:192–204.
- SANTIAPILLAI, C. 1992. Javan rhinoceros in Vietnam. *Pachyderm* 15: 25–27.
- SANTIAPILLAI, C., P. M. GIAO, AND V. V. DUNG. 1993a. Conservation and management of Javan rhino (*Rhinoceros sondaicus annamiticus*) in Vietnam. *Tiger Paper* 20:7–15.
- SANTIAPILLAI, C., P. M. GIAO, AND V. V. DUNG. 1993b. Conservation and management of Javan rhino (*Rhinoceros sondaicus*) in Vietnam. Pp. 248–256 in *Proceedings of an international conference: rhinoceros biology and conservation* (O. A. Ryder, ed.). Zoological Society of San Diego, San Diego, California.
- SANTIAPILLAI, C., AND H. SUPRAHMAN. 1986. The proposed translocation of the Javan rhinoceros *Rhinoceros sondaicus*. *Biological Conservation* 38:11–19.
- SCHALLER, G. B., N. X. DANG, L. D. THUY, AND V. T. SON. 1990. Javan rhinoceros in Vietnam. *Oryx* 24:77–80.
- SCHAURTE, W. T. 1968. Threatened species of rhinoceros in tropical S.E. Asia. Pp. 284–293 in *Conference on conservation in tropical south east Asia* (L. M. Talbot, et al., ed.). International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.
- SCHENKEL, R., AND L. SCHENKEL-HULLIGER. 1969a. The Javan rhinoceros (*Rh. sondaicus* Desm.) in Ujung Kulon Nature Reserve. Its ecology and behaviour. *Field study 1967 and 1968*. *Acta Tropica* 26:97–135.
- SCHENKEL, R., AND L. SCHENKEL-HULLIGER. 1969b. The last remnants of the Javan rhinoceros in Ujung Kulon Nature Reserve, Java. *Biological Conservation* 2:68–70.
- SCHENKEL, R., L. SCHENKEL-HULLIGER, AND W. S. RAMONO. 1978. Area management for the Javan rhinoceros [*Rhinoceros sondaicus* Desm.], a pilot study. *Malayan Nature Journal* 31:253–275.
- SCHUHMACHER, E. 1967. The last paradises: on the track of rare animals. Doubleday & Company, Inc., Garden City, New York.
- SCLATER, P. L. 1874. Announcement of the arrival in the Society's menagerie of a Javan rhinoceros. *Proceedings of the Zoological Society of London* 1874:182–183.
- SCLATER, P. L. 1876a. Exhibition and remarks upon a skin of a young rhinoceros from the Sunderbunds. *Proceedings of the Zoological Society of London* 1876:751.
- SCLATER, P. L. 1876b. On the rhinoceroses now or lately living in the Society's menagerie. *Transactions of the Zoological Society of London* 9:645–660 + plates xcv–xcix.
- SHOSHANI, J., AND J. F. EISENBERG. 1982. *Elephas maximus*. *Mammalian Species* 182:1–8.
- SODY, H. J. V. 1959. Das Javanische Nashorn *Rhinoceros sondaicus* historisch und biologisch. *Zeitschrift für Säugetierkunde* 24: 109–240.
- SOKOLOV, V. E. 1974. *Saiga tatarica*. *Mammalian Species* 38:1–4.
- SRIYANTO, A., AND M. HARYONO. 1997. Pengelolaan, strategi dan rencana tindakan konservasi badak Jawa di Taman Nasional Ujung Kulon. *Media Konservasi Edisi Khusus* 1997:75–81.
- STANLEY PRICE, M. R. 1993. What will it take to save the rhino? Pp. 48–68 in *Proceedings of an international conference: rhinoceros biology and conservation* (O. A. Ryder, ed.). Zoological Society of San Diego, San Diego, California.
- STEINMETZ, R. 2004. Gaur (*Bos gaurus*) and banteng (*B. javanicus*) in the lowland forest mosaic of Xe Pian Protected Area, Lao PDR: abundance, habitat use, and conservation. *Mammalia* 68:141–157.
- SUNQUIST, M. E., AND F. C. SUNQUIST. 2009. Family Felidae. Pp. 54–169 in *Handbook of the mammals of the world*. Vol. 1. Carnivores (D. E. Wilson and R. A. Mittermeier, eds.). Lynx Edicions, Barcelona, Spain.
- TALBOT, L. M. 1960. A look at threatened species: a report on some animals of the Middle East and southern Asia which are threatened with extermination. *Fauna Preservation Society*, London, United Kingdom.
- TALUKDAR, B. K., K. CROSBIE, S. ELLIS, W. S. RAMONO, A. C. WILLIAMS, AND SECTIONOV (EDS). 2009. Report on the meeting for conservation of Sumatran and Javan rhino in South East Asia. *Asian Rhino Specialist Group*, Guwahati, Assam, India.
- THOM, W. S. 1935. Rhinoceros shooting in Burma. *Journal of the Bombay Natural History Society* 38:138–150.
- TIMMINS, R. J., J. W. DUCKWORTH, S. HEDGES, R. STEINMETZ, AND A. PATTANAVIBOOL. 2008. *Bos javanicus*. International Union for the Conservation of Nature and Natural Resource's Red list. Gland, Switzerland. www.iucnredlist.org, accessed 19 February 2010.
- TIURIA, R., ET AL. 2006. Identification of endoparasites from faeces of Javan rhino (*Rhinoceros sondaicus*) in Ujung Kulon National Park, Indonesia. *Proceedings of the Asian Zoo and Wildlife Medicine Convention* 2006:31.
- TOUGARD, C., T. DELEFOSSE, C. HÄNNI, AND C. MONTGELARD. 2001. Phylogenetic relationships of the five extant rhinoceros species (Rhinocerotidae, Perissodactyla) based on mitochondrial cytochrome *b* and 12S rRNA genes. *Molecular Phylogenetics and Evolution* 19:34–44.
- UNITED STATES FISH AND WILDLIFE SERVICE. 1970. Conservation of endangered species and other fish or wildlife. *Federal Register* 35(106):8491–8498.
- U. TUN YIN 1954. A note on the position of rhinoceros in the Union of Burma (1953). *Journal of the Bombay Natural History Society* 52: 83–87.
- U. TUN YIN 1956. A supplementary note on the status of rhinoceros in the Union of Burma—1955. *Journal of the Bombay Natural History Society* 53:257–258.
- U. TUN YIN 1967. *Wild animals of Burma*. Rangoon Gazette, Limited, Rangoon, Burma.
- VAGELER, P. 1927. Ein neues Rhinoceros. *Die Umschau* 31:289–290.
- VAN MERM, R. H. 2008. Ecological and social aspects of reintroducing megafauna: a case study on the suitability of the Honje Mountains as a release site for the Javan rhinoceros (*Rhinoceros sondaicus*). M.S. thesis, Saxion Universities of Applied Sciences, Deventer, Netherlands, and University of Greenwich, London, United Kingdom.
- VAN STRIEN, N. J. 1978. On the difference in the footprints of the Javan and the Sumatran rhinoceros. *Tiger Paper* 51:16–19.
- VAN STRIEN, N. J., ET AL. 2008. *Rhinoceros sondaicus*. International Union for the Conservation of Nature and Natural Resource's Red list, Gland, Switzerland. www.iucnredlist.org, accessed 14 February 2010.
- VAN STRIEN, N. J., AND K. ROOKMAAKER. 2010. The impact of the Krakatoa eruption in 1883 on the population of *Rhinoceros sondaicus* in Ujung Kulon, with details of rhino observations from 1857 to 1949. *Journal of Threatened Taxa* 2:633–638.
- VON KOENIGSWALD, G. H. R. 1933. Beiträge zur Kenntnis der fossilen Säugetierfauna Javas. *Wetenschappelijke Mededelingen Dienst van den Mijnbouw in Nederlandsch-Indië* 23:1–185.
- VON MARTENS, E. 1876. Die Preussische Expedition nach Ost-Asien. Nach Amtlichen Quellen. *Zoologischer Theil*. Erster Band. Allgemeines und Wirbelthiere. Verlag der Königlichen Geheimen Ober-Hofbuchdruckerei, Berlin, Germany.
- VON MUGGENTHALER, E. K., J. W. STOUGHTON, AND J. C. DANIEL, JR. 1993. Infrasound from the Rhinocerotidae. Pp. 136–140 in *Proceedings of an international conference: rhinoceros biology and conservation* (O. A. Ryder, ed.). Zoological Society of San Diego, San Diego, California.
- WEIGL, R. 2005. Longevity of mammals in captivity; from the living collections of the world. *Kleine Senckenberg-Reihe* 48:1–214.
- WILLERSLEV, E., ET AL. 2009. Analysis of complete mitochondrial genomes from extinct and extant rhinoceroses reveals lack of phylogenetic resolution. *BMC Evolutionary Biology* 9:95.
- WORLD CONSERVATION MONITORING CENTRE. 2005. Ujung Kulon National Park & Krakatau Nature Reserve, Java, Indonesia. United Nations Environment Programme, New York. <http://www.unep-wcmc.org/sites/wh/pdf/Ujung%20Kulon.pdf>, accessed 24 April 2010.
- WURSTER, D., AND K. BENIRSCHKE. 1968. The chromosomes of the great Indian rhinoceros. *Experientia* 24:511.

Associate editor of this account was DAVID ZEGERS. PAMELA OWEN reviewed the fossil account and ALFRED L. GARDNER reviewed the synonymy. Editor was MEREDITH J. HAMILTON.