

18. Rhinocerotids from the Siwalik record

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Introduction

This chapter provides a synthetic survey of the rhinocerotid record in the Siwalik faunal sequence (taxa and assemblages, taxonomic diversity, body-weight estimates, and ecological inferences).

Rhinocerotidae have by far the longest temporal range among South Asian perissodactyls: the earliest representatives are recorded in the late middle Eocene of Myanmar and Vietnam (Holroyd et al., 2006; Böhme et al., 2014) and their record is then virtually uninterrupted, culminating in three Recent Asian species (Laurie et al., 1983; Antoine, 2012). By contrast, other Rhinocerotidae, such as Hyracodontidae (including giant rhinos, better known as indricotheres or baluchitheres) and Amyndodontidae (hippo-like amphibious forms) co-occurred with rhinocerotids in South Asia, but are restricted to the Paleogene period (Antoine et al., 2004, 2013). Rhinocerotids were particularly diverse and abundant throughout the Neogene in South Asia (e.g., Antoine & Welcomme, 2000; Antoine, 2012; Antoine et al., in press). Several comprehensive studies concerning the Siwalik Rhinocerotidae were published in the 19th century (Falconer & Cautley, 1846-1849; Lydekker, 1881, 1884, 1886) and early 1900s (Pilgrim, 1908, 1910, 1912, 1913; Matthew, 1929; Forster Cooper, 1934; Colbert, 1934, 1935). However, and with a few notable exceptions (Heissig, 1972; Guérin in Pilbeam et al., 1979; Khan et al., 2011, 2014), alpha-taxonomy of the Siwalik rhinocerotids has long been underinvestigated, despite intense field work in the Potwar Plateau in the 1970–2000s. In nearby areas, such as the Sulaiman Province of Pakistan, rhinocerotids were closely investigated in recent decades, based on new field collections from the Zinda Pir and the Bugti Hills (Antoine & Welcomme, 2000; Antoine, 2002; Raza et al., 2002; Antoine et al., 2003a, 2003b, 2010, 2013).

Material and methods

35

36 The current study is based mainly on specimens from the Lower and Middle Siwaliks of the
37 Potwar Plateau, collected by the Geological Survey of Pakistan-Yale, later Harvard Peabody
38 Museum joint expeditions in the last decades, and presently curated either in the Harvard
39 University Paleontology Laboratory, Cambridge (HUPL; ~720 specimens), in the
40 *Collections de Paléontologie*, Muséum National d'Histoire Naturelle in Paris (MNHN; 59
41 specimens), or in the Palaeontology Department of the Pakistan Museum of Natural History
42 in Islamabad (PMNH; 1973-1980 field seasons; ~50 specimens). Siwalik specimens described
43 by Matthew (1929), Forster Cooper (1934), Colbert (1934, 1935), and Heissig (1972), and
44 curated in the American Museum of Natural History (AMNH; New York), the Natural
45 History Museum (NHM; London), and the Bayerische Staatssammlung für Paläontologie und
46 Geologie (BSP; Munich), were also studied. Material stored in the Indian Museum in Calcutta
47 was not studied.

48 Comparative material primarily consists of specimens from Neogene deposits of nearby areas
49 in Pakistan (Bugti Hills: MNHN and Muséum d'Histoire naturelle in Toulouse, France; Zinda
50 Pir: HUPL). Undescribed Thai material stored in the Rajabhat Institute (Nakhon Ratchasima)
51 and the Sahat Sakhan Dinosaur Centre (Sahat Sakhan, Kalasin) was also useful for
52 comparison. Stratigraphy and taxonomy of other South Asian rhinocerotid occurrences were
53 cautiously surveyed from the literature. Figure 1 illustrates the main rhinocerotid-yielding
54 localities and areas whilst Table 18.2 reports the stratigraphic ranges of documented taxa.
55 Body weights were estimated using both dental (area of m1: Legendre, 1989; length of M1,
56 M2, and M3: Fortelius & Kappelman, 1993) and postcranial dimensions (astragalus:
57 Tsubamoto, 2014), or were extrapolated from those of present-day rhinoceroses (Guérin,
58 1980: *Rhinoceros* aff. *sondaicus* and *Rhinoceros* aff. *sivalensis*). Raw estimates appear in the
59 Table 18.1 and mean values for each documented taxon are reported in Table 18.2. The
60 available material did not allow for characterizing sexual dimorphism or intraspecific body-
61 weight changes through time.

62

63 **Systematic overview of Siwalik rhinocerotids**

64

65 Most rhinocerotid groups known in the Old World are found in Neogene deposits of Siwaliks
66 and adjacent areas (Table 18.2). The relationships among Siwalik rhinocerotids recognized at
67 the species level, as reported in Fig. 18.2, are mapped on formal phylogenetic trees based on
68 Antoine et al. (2003b, 2010) and Becker et al. (2013). Elasmotheriinae are represented by

69 only one species of Elasmotheriina; in sharp contrast, Rhinocerotinae are quite diverse
70 throughout the studied interval, with at least 12 species referred to Aceratheriina,
71 Teleoceratina, and Rhinocerotina (Fig. 18.2).

72
73 The **Elasmotheriina**, from the Miocene–Pleistocene of Eurasia and the Miocene of Africa,
74 were considered as the sister group of the Rhinocerotina until phylogenetic analyses
75 demonstrated that this clade was more closely related to North American Diceratheriini and
76 Menoceratina, within Elasmotheriinae, with an early differentiation from Rhinocerotinae (Fig.
77 18.2; Antoine, 2002; Antoine et al., 2003b). Early elasmotheriines were tapir-sized, slender-
78 limbed rhinos; some of them had small nasal horns, whilst the latest representatives of this
79 clade were mammoth-sized, with a huge frontal horn and ever-growing teeth (e.g., Pleistocene
80 *Elasmotherium*; Antoine, 2002).

81 The only elasmotheriine recognized in the Siwalik faunal sequence is *Caementodon*
82 *oettingenae* Heissig, 1972, an early-diverging taxon thus far recorded in the Chinji and Nagri
83 formations of the Potwar Plateau (Heissig, 1972; Antoine, 2002). New data extend its
84 stratigraphic range later to the lower Dhok Pathan Formation (8.6 Ma; Table 18.2) and earlier
85 to the middle Kamli Formation (15.1 Ma). Around 50 cranial, dental, and postcranial
86 remains are recognized, originating from 30 localities (body weight ~810 kg; Fig. 18.3A-B,
87 18.4A). The earliest elasmotheriine, *Bugtirhinus praecursor* Antoine & Welcomme, 2000, is
88 smaller (body weight ~480 kg), restricted to the lowermost Miocene deposits of Sulaiman
89 Province (Fig. 18.5; Antoine et al., 2013), attesting to the importance of the Indian
90 Subcontinent in the early evolution of this clade. A close relative of this taxon was recently
91 described from coeval deposits from Vietnam (*Bugtirhinus* sp.; Prieto et al., 2018).

92
93 Among Aceratheriini Rhinocerotinae, **Aceratheriina** are hornless extinct rhinos, widespread
94 in the Oligocene–Miocene of North America and Eurasia, as well as in the Miocene of Africa
95 (e.g., Geraads, 2010). Most of them are slender-limbed, tetradactyl, and brachydont, even
96 though a small group known as chilothers developed short-limbs and high-crowned teeth
97 (e.g., Antoine et al., 2003b).

98 At least two taxa from the Lower and Middle Siwaliks document the genus *Alicornops*
99 Ginsburg & Guérin, 1979, the representatives of which lack the enlarged hippo-like
100 symphysis typical of more derived Asian genera such as *Chilotherium* Ringström, 1924 and
101 *Acerorhinus* Kretzoi, 1942. “*Aceratherium* sp.” from the Chinji Formation (Heissig, 1972)
102 and “*Alicornops* sp., cf. *A. simorreense*” from the upper Nagri Formation/lower Dhok Pathan

103 Formation (Guérin, in Pilbeam et al., 1979) probably belong to the same taxon, which can be
104 provisionally designated as *Alicornops* cf. *simorreense* (body weight ~880 kg; Fig. 18.5). This
105 taxon is documented by a single metatarsal from Y478 (14.1 Ma), in the collections surveyed
106 here. This occurrence is coeval with the maximal abundance of *A. simorreense* in Europe
107 (Heissig, 2012). The other species is *Alicornops complanatum* (Heissig, 1972), which is much
108 better represented and occurs throughout the Dhok Pathan Formation in the Potwar Plateau
109 (Colbert, 1935; Heissig, 1972; new data) and in coeval deposits of the Bugti Hills (Antoine et
110 al., 2003b). The specimens examined span a 16.8–8.0 Ma interval and consist of 33 cranio-
111 mandibular, dental, and postcranial remains from eight localities (mainly Y450 and Y545;
112 Fig. 18.3C, 18.4B). Body weight approximates 820 kg. The upper Dhok Pathan specimens
113 described by Heissig (1972) and referable to *A. complanatum* would be among the last
114 occurrences of aceratheriines throughout Eurasia, but their numeric age is not constrained.
115 Sixteen mandibular, dental, and postcranial specimens were assigned to *Alicornops* sp., *faute*
116 *de mieux*. They first occur at 16.8 Ma (i.e., earlier than the FAD of *Alicornops* in Europe,
117 estimated at ca. 15.0 Ma; Antoine et al., 2003b) and are likely to document another
118 representative of *Alicornops* in the Siwalik faunal sequence.

119

120 **Teleoceratina** are hippo-like extinct Rhinocerotini, closely related to Rhinocerotina (Fig.
121 18.2). Most of them had hornless skulls, barrel-shaped bodies, and shortened limbs adapted to
122 swamps and riverbanks. Teleoceratines span the late Oligocene–latest Miocene interval in
123 Eurasia, the Miocene epoch in Africa, and the early Miocene–early Pliocene in North and
124 Central America (Prothero, 2005; Sizov et al., in press). Most teleoceratines are interpreted as
125 browsers based on both dental morphology and isotopic studies (MacFadden, 1998).
126 Available isotopic data on Siwalik teleoceratines indicate a C₃ plant diet, consistent with this
127 interpretation (see Chapter 24, this volume). All three teleoceratine species formally
128 recognized in the Siwalik sequence are long-lived (~10 My) and widely co-occurred
129 throughout their ranges.

130 After long controversies regarding its generic assignment, the puzzling “*Rhinoceros*
131 *sivalensis intermedius* Lydekker, 1884”, from the Chinji and Nagri formations, was referred
132 to as “*Chilotherium intermedium intermedium*” by Heissig (1972), i.e., considered a short-
133 limbed aceratheriine. A later formal phylogenetic analysis instead allocated its holotype to the
134 Teleocerotina (Antoine et al., 2003b: fig. 4). Amongst the 42 undescribed specimens
135 unambiguously documenting this taxon in the Siwalik faunal sequence between 17.9–8.0 Ma
136 (10 localities), 27 dental and postcranial remains found in association at Y678 (same

137 individual) confirm its assignment to teleoceratines (Fig. 18.3D, 18.4C-D). These specimens
138 further point to the early-diverging genus *Diaceratherium*, closely recalling those of the early
139 Miocene *D. aginense* from Western Europe, based on postcranial traits (slender zeugopods
140 and autopods) (e.g., Répelin, 1917), and testifying to the survival of long-limbed
141 teleoceratines in South Asia long after their supposed demise elsewhere in Eurasia. A recent
142 phylogenetic analysis of Eurasian teleoceratines concludes to the assignment of both species
143 to *Brachydiceratherium* Lavocat, 1951 (hereafter *Bd.*), whereas the genus *Diaceratherium*
144 should be restricted to its type species, *D. tomerdingense* Dietrich, 1931 (Sizov et al., in
145 press). I therefore consider here the binomen *Brachydiceratherium intermedium* (Lydekker,
146 1884). Body weight is estimated at ~1,900 kg. A close ally of *D. intermedium*, showing
147 similar postcranial features, occurs in the late early Miocene Tagay assemblage of Olkhon
148 Island, in Siberia (Sizov et al., in press). The Pliocene occurrence of “*C. intermedium*”, as
149 mentioned by Patnaik (2013) in the Siwaliks of India, is not reliable. Two larger
150 teleoceratines are recorded in the Siwalik faunal sequence. These similarly long-ranged (>10
151 My) and widely co-occurring species were the most abundant Miocene rhinos in the Potwar
152 Plateau. *Brachydiceratherium fatehjangense* (Pilgrim, 1910) has a continuous record in the
153 Siwalik sequence, is documented by 44 cranio-dental and postcranial remains from 29
154 localities (Fig. 18.3E, 18.4E), and spans the Kamliāl–Dhok Pathan interval (17.9–7.4 Ma). Its
155 body weight was ~2,000 kg. Only three specimens (6.8%) belong to juvenile individuals. The
156 FAD of this species dates back to the earliest Miocene in central Pakistan (Fig. 18.5; Antoine
157 et al., 2013). In the Siwalik sequence of Jammu Sub-Himalaya, India, *Bd. fatehjangense*
158 occurs in lower Murree sediments (early Miocene; Patnaik, 2013); Chavasseau et al. (2006)
159 report *Bd. fatehjangense* in the middle Miocene Chaungtha locality of central Myanmar
160 (Irrawaddy Formation; Fig. 1).

161 *Brachypotherium perimense* (Falconer & Cautley, 1847) is the largest and heaviest
162 teleoceratine ever known (mean body weight of ~3,710 kg with some individuals
163 (over)estimated at 6,100 kg; Table 18.1, 18.2) with extremely short carpals and tarsals (Fig.
164 18.3F, 18.4F). This species was coeval with *Bd. fatehjangense*, but occurred more widely in
165 the Siwalik sequence. It is recognized from 180 cranio-mandibular, dental, and postcranial
166 remains from 62 localities (18.0–7.2 Ma). Juveniles, subadults, and adults are represented by
167 20 (11.1%), three (1.7%), and 154 specimens (87.2%), respectively. Within the rhinocerotid
168 record from the Potwar Plateau, *B. perimense* follows the closest age distribution with respect
169 to natural populations of recent rhinoceroses (Chitwan Park; Laurie et al., 1983).

170 *Brachypotherium perimense* was originally described by Falconer (1845) from the late

171 Miocene of Perim Island, in Gujarat, western India (Fig. 1; today “Piram Island”; Chauhan,
172 2008). This huge species is also documented in the early–late Miocene interval in the
173 Sulaiman Province (Fig. 18.4; Antoine et al., 2013), in middle Miocene deposits of the Dang
174 Valley in Nepal (Surai Khola; Corvinus & Rimal, 2001), in the Siwaliks of India (13.2–9.8
175 Ma; Patnaik, 2013) and in upper Miocene localities of Central Thailand (Chaimanee et al.,
176 2004).

177
178 **Rhinocerotina** are medium to large sized rhinos with modern representatives living either in
179 riversides and moist forests (Asian rhinos; Antoine, 2012) or savannahs (African rhinos;
180 Guérin, 1980). All five living rhino species belong to this clade; three live in South Asia, of
181 which two have only a nasal horn: the large *Rhinoceros unicornis* (Indian rhino) and the lesser
182 *R. sondaicus* (nearly extinct Javan rhino). The third, *Dicerorhinus sumatrensis* (Sumatran
183 rhino), also has a frontal horn, like African rhinos (*Diceros bicornis* and *Ceratotherium*
184 *simum*, black and white rhino, respectively). The fossil record of Rhinocerotina is so far
185 restricted to the Old World and this clade is particularly well represented in the Siwalik faunal
186 sequence (Fig. 18.2). Among Rhinocerotidae, only Rhinocerotina have a well constrained
187 record after the Miocene-Pliocene transition in the Siwalik record. Limited stable isotope data
188 suggest that Miocene rhinocerotines foraged on C3 plants (see Chapter 24 for details).
189 *Gaindatherium* Colbert, 1934 groups medium-sized and one-horned rhinocerotines, closely
190 related to *Lartetotherium* Lartet, 1837, from the late early–early late Miocene of Europe
191 (Antoine et al., 2003b, 2010). At least two representatives of *Gaindatherium* occur throughout
192 the Miocene epoch in the Potwar Plateau: *Gaindatherium browni* Colbert, 1934 is
193 documented through 75 dental and postcranial remains (Fig. 18.3G, 18.4G-H), with a
194 temporal range from at least 16.5–8.7 Ma (25 localities). (The age of the oldest locality is not
195 well-constrained, see Table 18.2.) Most specimens represent adults (72/75 = 96%). Estimated
196 body weight is ~1,070 kg. The sample studied by Heissig (1972) was restricted to the middle
197 Miocene Chinji Formation, while Patnaik (2013) provides a 12.7–8.85 Ma range for this
198 species in the Siwaliks of India. Compared to *G. browni*, its sister species *G. vidali* Heissig,
199 1972, is slightly smaller (body weight ~830 kg; Fig. 18.3H, 18.4I) with more slender
200 proportions in the appendicular skeleton (corresponding to Rhinocerotini type 2 and type 1 of
201 Heissig (1972), respectively). In good agreement with Heissig (1972), *G. vidali* is also less
202 abundant than *G. browni*, with 16 dental and postcranial remains from 12 localities (ranging
203 from 14.1–8.0 Ma). The two species have concurrent ranges and they co-occur in four
204 localities (Y76, Y311, Y502, and Y647; Fig. 18.5). *Gaindatherium vidali* was originally

205 reported only from the early late Miocene Nagri Formation from the Potwar Plateau (Heissig,
206 1972), but Khan et al. (2011) have described some remains from the middle Miocene Chinji
207 Formation. Due to considerable morphological and metric overlap between the two species,
208 58 dental and postcranial specimens were assigned only to *Gaindatherium* sp. (Fig. 18.3I),
209 with a first local occurrence at 17.9 Ma (Y747). *Gaindatherium* cf. *browni*, recorded in ~21
210 Ma deposits of the Chitarwata Formation in the Bugti Hills, provides the FAD for the genus
211 (Fig. 18.5; Antoine et al., 2013). Its body weight approximates 810 kg.

212 Close allies or putative representatives of the living genera *Rhinoceros* and *Dicerorhinus* have
213 also been recognized in the Siwalik sequence. Ten dental and postcranial remains from two
214 localities of the Kamli Formation (Y744 and Y592; Fig. 18.3J, 18.4J) attest to the presence
215 of a large one-horned rhinocerotine during the late Early Miocene in the Potwar Plateau
216 (16.7–16.0 Ma). This taxon is most likely conspecific with “cf. *Rhinoceros* sp.” as recognized
217 in the 19 Ma Assemblage B of the Sulaiman Province (Fig. 18.5; Antoine et al., 2013). Its
218 body weight is estimated at ~1,740 kg (Table 18.2). A small isolated DP1 from the Y311
219 locality (YGSP 10466; 10.1 Ma) documents an early relative of the lesser one-horned rhino,
220 namely *Rhinoceros* aff. *sondaicus*, as described in coeval deposits of the Nagri Formation by
221 Heissig (1972). The size of this tooth indicates a body weight of ~1,500 kg. A larger
222 representative of *Rhinoceros* is recorded in four localities in the interval between 8.9–8.0 Ma,
223 through 34 dental and postcranial specimens (30 of which belong to the same individual;
224 YGSP 49617 at Y897). Their general dimensions yield body-weight estimates of
225 approximately 2,000 kg (Fig. 18.3K, 18.4K). These remains strongly resemble those assigned
226 to *Rhinoceros* aff. *sivalensis* by Heissig (1972) in the Dhok Pathan Formation and in coeval
227 deposits from the Bugti Hills (~8.5 Ma; Antoine et al., 2013). *Rhinoceros sivalensis* Falconer
228 & Cautley, 1847 occurs in early Pleistocene deposits of Pakistan and India (see Patnaik, 2013)
229 and a latest Miocene–Pliocene ghost lineage might be inferred for this taxon in the Himalayan
230 foothills (Raza et al., 1984).

231 A palate, three isolated upper premolars, and six slender postcranial bones of small to medium
232 dimensions were attributed to a close ally of the two-horned Sumatran rhino, *Dicerorhinus*
233 aff. *sumatrensis* (Fig. 18.3L, 18.4L). The fossils come from five localities from the Chinji and
234 Nagri formations, with a temporal range of 13.7–10.1 Ma (Fig. 18.5). Body weight is
235 estimated at ~1,230 kg. The same taxon was previously described in the Chinji Formation
236 (Heissig, 1972). The remains from the middle and upper Chinji Formation, referred to as
237 “*Didermocerus* cf. *abeli*” by Heissig (1972), probably document *Dicerorhinus* aff.

238 *sumatrensis* instead of “*Aceratherium abeli* Forster-Cooper, 1934”, an enigmatic rhinocerotid
239 restricted to Oligocene layers from the Bugti Hills (Antoine et al., 2013: 417).

240 Another putative two-horned rhinocerotine was documented in upper Miocene deposits (8.0–
241 7.4 Ma), based on an isolated M3 (Fig. 18.3M) and five postcranial bones of large dimensions
242 (four bones belong to the same right hand; Fig. 18.4M), were assigned to *Ceratotherium*
243 *neumayri* (Osborn, 1900). This species was widespread throughout the eastern Mediterranean
244 in the late Miocene, with maximum abundance around 9–8 Ma (e.g., Antoine et al., 2012).
245 The body weight of *C. neumayri* was around 2,500 kg (Table 18.1). It is recognized for the
246 first time in the Siwalik faunal sequence in this summary.

247 Other rhinocerotine taxa from the Upper Siwaliks of Pakistan and India (late Pliocene–early
248 middle Pleistocene), such as *Rhinoceros palaeindicus* Falconer & Cautley, 1847 (junior
249 synonym of *R. unicornis*; e.g., Laurie et al., 1983; Antoine, 2012) and *Rhinoceros platyrhinus*
250 Falconer & Cautley, 1847 (for a review, see Pandolfi & Maiorino, 2016), have not been
251 recognized in material currently available. Until recently, all three extant Asian rhinos were
252 present in the Indian Himalayan foothills (e.g., Antoine, 2012). *R. unicornis* was widespread
253 in the late Pleistocene of peninsular India (Chauhan, 2008). It no longer occurs in Pakistan,
254 but it is still living in India, Nepal, and Bhutan (Antoine, 2012).

255

256 **Rhinocerotid diversity and body-weight changes throughout the Siwalik sequence**

257

258 When considered as part of one paleobiogeographic province, the Potwar Plateau (Kamlial
259 Formation–Middle Dhok Pathan Formation; Barry et al., 2002, 2013) and
260 Sulaiman Province (Barry et al., 2005; Antoine et al., 2013) together provide an exceptional
261 overview of rhinocerotid diversity and evolutionary dynamics for the Neogene interval in
262 South Asia. Regarding the subsequent interval (latest Miocene–?Early Pliocene; Upper Dhok
263 Pathan Formation; see below), no chronostratigraphic constraint is available for
264 rhinocerotid remains described by Heissig (1972). Moreover, a reliable taxonomic revision of
265 Upper Siwalik rhinocerotines is badly needed (these taxa are gathered under the name
266 ‘*Rhinoceros* spp.’; Fig. 18.5). Hence, the last seven million years of Siwalik rhinocerotids are
267 not discussed further here.

268 Regardless of the number of suprageneric groups considered, there are two intervals of high
269 species diversity (Fig. 18.5). They are not obviously correlated with the number of localities
270 documenting a given timeslice in the Potwar Plateau (Fig. 18.5, right columns). However,

271 they might be linked to ecological factors (such as climate and food supply), as discussed
272 below.

273 After a short interval with only three co-occurring species (23.0–22.7 Ma), there is a diversity
274 peak in the early Miocene (Aquitanian and earliest Burdigalian times, 22.7–19.5 Ma), with 8–
275 10 coeval species recorded in the Bugti Hills. This interval coincides with warm, moist
276 climatic conditions and the presence of extensive tropical forests in South Asia. Such an
277 ecosystem could support species-rich browser-dominated herbivore guilds as documented in
278 Sulaiman Province (e.g., Antoine et al., 2013) and supported by isotopic analyses of tooth
279 enamel (e.g., Martin et al., 2011). During this interval, the distribution of body weights is
280 evenly distributed and balanced within a 150–2,000 kg domain. Four estimated species
281 weights are less than 1,000 kg (the tapir-sized *Protaceratherium* sp.: 150 kg; *Bugtirhinus*
282 *praecursor*: ~480 kg; *Plesiaceratherium naricum*: ~550 kg; *Gaindatherium* cf. *browni*: ~810
283 kg; Table 18.1), whereas *Pleuroceros blanfordi* (~1,530 kg), *Mesaceratherium welcommi*
284 (~1,620 kg), and teleoceratines are much heavier (*Prosantorhinus shahbazi*: ~1,220 kg;
285 *Brachypotherium gajense*: ~1,920 kg; *Brachydiceratherium fatehjangense*: ~2,000 kg).

286 Rhinocerotid species diversity then decreases gradually, with the possible presence of three
287 species between 18.7–18.0 Ma, hypothesized due to (i) a gap between the top of Assemblage
288 B in the Sulaiman Province (Antoine et al., 2013) and the base of the Kamliyal Formation in
289 the Potwar Plateau (Wang et al., 2013) and (ii) the relative paucity of Kamliyal localities
290 (Barry et al., 2013). In the species-poor interval from 19.0–16.7 Ma, a marked loss of small
291 body sizes and shift toward heavier body weights is recorded, with a range of 1,740–3,710 kg.
292 The lighter rhinocerotid is cf. *Rhinoceros* sp. (~1,740 kg; Table 18.1). Once again,
293 teleoceratines comprise the heavier component of the fauna, with *Brachydiceratherium*
294 *intermedium* (~1,900 kg; ‘replacing’ *B. gajense* in the assemblage), *Bd. fatehjangense* (~2,000
295 kg), and the first appearance of the heavy *B. perimense* (~3,710 kg).

296 The next stage (16.7–7.0 Ma) has species-rich assemblages, with the greatest body weight
297 range (810–3,710 kg). A second diversity peak following that of the Early Miocene occurs in
298 the early Late Miocene (11–10 Ma, lower Nagri Formation), with up to 12 co-occurring
299 species, despite low numbers of localities per time slice (Fig. 18.5; Barry et al., 2013). These
300 rhino assemblages are species-rich until 8.7 Ma (around eight species at the Nagri–Dhok
301 Pathan transition; Fig. 18.5), after which diversity decreases again to only two species at ~7
302 Ma (middle Dhok Pathan). This decline occurs in spite of high numbers of localities per time
303 slice (Fig. 18.5; Barry et al., 2013; Wang et al., 2013). This last interval coincides with the
304 replacement of wet monsoonal forest by dry woodland then by savannah (Badgley et al.,

305 2008). A salient feature of the 17.9–7.0 Ma interval, aside from the persistence of heavy,
306 water-dependent taxa, is the co-occurrence of four rhinocerotids having similar body weights
307 between 800–900 kg (*Caementodon oettingenae*: ~810 kg; *Alicornops complanatum*: ~820 kg;
308 *A. cf. simorreense*: ~880 kg; *Gaindatherium vidali*: ~830 kg), probably with distinct feeding
309 habits. For the rhinocerotines, body weights were non-overlapping over a wide range
310 (*Gaindatherium browni*: ~1,070 kg; *Dicerorhinus aff. sumatrensis*: ~1,230 kg; *Rhinoceros*
311 *aff. sondaicus*: ~1,500 kg; cf. *Rhinoceros sp.*: ~1,740 kg; *R. aff. sivalensis*: ~2,000 kg;
312 *Ceratotherium neumayri*: ~2,490 kg; Table 18.1).

313 In summary, throughout the sequence, taxonomic diversity is particularly unbalanced among
314 Rhinocerotidae, with only two species of Elasmotheriinae but over 20 species recognized for
315 Rhinocerotinae (Fig. 4). Most rhinocerotid species have long stratigraphic ranges in the
316 Siwalik faunal sequence (Fig. 18.5), with the notable exception of cf. *Rhinoceros sp.*,
317 *Rhinoceros aff. sondaicus* (if distinct from *R. sondaicus*) and *Ceratotherium neumayri*. The
318 elasmotheriines *Bugtirhinus praecursor* (23.0–19.5 Ma) and *Caementodon oettingenae* (15.1–
319 8.6 Ma) did not overlap. In addition, the ~4.4 My-long gap (no elasmotheriine in the Kamli-
320 Formation) implies that *C. oettingenae* is an early middle Miocene immigrant from
321 another Eurasian region (other representatives of *Caementodon* are known in the late early–
322 early middle Miocene of both the Caucasus and China; see Antoine, 2002). Early-diverging
323 Rhinocerotinae (*Protaceratherium sp.*, *Plesiaceratherium naricum*, *Pleuroceros blanfordi*,
324 and *Mesaceratherium welcommi*) comprise almost half of species richness during the earliest
325 interval (23–19 Ma; Fig. 18.5). They co-occur with *Bugtirhinus praecursor*, the earliest
326 representatives of Teleoceratina (either short-ranging [*Brachypotherium gajense* and
327 *Prosantorhinus shahbazi*] or long-ranging [*Bd. fatehjangense*]), and the first Rhinocerotina
328 (*Gaindatherium cf. browni* and cf. *Rhinoceros sp.*). Their gradual disappearance is the main
329 component of the diversity decrease following the early Miocene peak. A major turnover in
330 rhinocerotids occurs then, with the first local occurrence of the teleoceratines
331 *Brachypotherium perimense* and *Brachydiceratherium intermedium* (~18 Ma), followed by
332 the appearance of the rhinocerotine *Gaindatherium browni* (16.9 Ma) and the aceratheriine
333 *Alicornops sp.* (16.8 Ma) in the middle Kamli-Formation. Rhinocerotid assemblages are
334 then stable, with only the first occurrence of *Caementodon oettingenae* at 15.1 Ma and the
335 disappearance of cf. *Rhinoceros sp.* (12.4 Ma) as noticeable events. Afterwards, diversity
336 increases to reach a peak between 11–10 Ma, with representatives of all suprageneric groups
337 among Rhinocerotidae (Elasmotheriina: *Caementodon oettingenae*; Aceratheriina: *Alicornops*
338 cf. *simorreense* and *A. complanatum*; Teleoceratina: *Brachydiceratherium intermedium*, *Bd.*

339 *fatehjangense*, and *Brachypotherium perimense*; Rhinocerotina: *Gaindatherium browni*, *G.*
340 *vidali*, *Rhinoceros* aff. *sondaicus*, *R.* aff. *sivalensis*, and *Dicerorhinus* aff. *sumatrensis*). In
341 younger intervals, species richness decreases gradually until the last rhinocerotid record
342 surveyed here (7.2 Ma). The immigrant *Ceratotherium neumayri* is briefly present in the 8.0–
343 7.4 Ma interval, and may be from the Eastern Mediterranean, where it is a conspicuous
344 element of Tortonian mammalian faunas (e.g., Antoine et al., 2012). The persistence of
345 *Rhinoceros* aff. *sivalensis*, *Alicornops complanatum*, and *Brachypotherium perimense* in
346 deposits from the Upper Dhok Pathan Formation (latest Miocene–early Pliocene) was
347 described by Heissig (1972). They probably document the last occurrences of both
348 Aceratheriina and Teleoceratina on a global scale, but their age is not well constrained
349 chronostratigraphically. Although a few localities document this stratigraphic interval (Fig.
350 18.5; Barry et al., 2013), rhinocerotid remains are not present in the available sample
351 (presently curated at HUPL or MNHN).

352

353 **Conclusion**

354 The analysis of ~2,000 cranio-mandibular, dental, and postcranial specimens from Miocene
355 deposits of Pakistan (~800 from the Potwar Plateau and 1,200 from Sulaiman Province)
356 allows the recognition of more than 20 rhinocerotid species. The major identified turnover
357 between 18.7–18.0 Ma consists of the demise of early-diverging representatives of
358 Rhinocerotinae and the onset of assemblages including two or three small aceratheriines, two
359 or three large teleoceratines, and up to eight small to large rhinocerotines (from 18–7 Ma). In
360 the Potwar Plateau, rhinocerotid species richness increases regularly from the earliest Kamli
361 record to reach a peak at 11–10 Ma, with 12 coeval species (mostly browsers). One-horned
362 and two-horned rhinocerotines and their sister taxa (hippo-like teleoceratines) dominate the
363 megaherbivore guilds throughout the 18–7 Ma interval, under humid, then drier
364 environmental conditions. Notably, this study confirms the teleoceratine affinities of
365 “*Rhinoceros sivalensis intermedius* Lydekker, 1884”, here designated as
366 *Brachydiceratherium intermedium* (Lydekker, 1884), and includes the first recognition of the
367 large two-horned rhinocerotine *Ceratotherium neumayri* in South Asia. A thorough
368 taxonomic revision of rhinocerotid remains originating from younger intervals of the Upper
369 Siwaliks would be critically important, especially for better constraining the final demise of
370 stem-rhinocerotids and the emergence of modern Asian rhinoceroses.

371

372

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383

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548 **Table 18.1** Body-weight estimates for rhinocerotid taxa recognized in the Siwalik faunal
549 sequence of the Potwar Plateau (bold-font binomial names) and in Miocene deposits of
550 Sulaiman Province. Estimates were primarily calculated based on the length of M1, M2, or
551 M3 (Fortelius & Kappelman, 1993), the area of m1 (Legendre, 1989), and the trochlear width
552 of the astragalus (Tsubamoto, 2014), with minimum-maximum ranges provided whenever
553 possible. Estimates and mean values are given in kg. Standard Deviations are provided in
554 square brackets.
555

Taxon	Body Weight (kg)	Reference	Specimen	Mean value (kg) and [SD]
<i>Bugtirhinus</i>	334	pers. obs.	m1 NHM w/n (min)	
<i>praecursor</i>	412	pers. obs.	m1 NHM M15345 (max)	
	460	pers. obs.	M3 Pak 762	477
	517	pers. obs.	M1 NHM M15361	[94]
	571	pers. obs.	M2 NHM M15361	
	571	Antoine & Welcomme (2000)	Astragalus Pak 788	
<i>Caementodon</i>	368	pers. obs.	Astragalus 1956 II 385 (min)	
<i>oettingenae</i>	571	pers. obs.	Astragalus YGSP 40848 (max)	
	597	pers. obs.	M3 CH 018	
	658	pers. obs.	m1 YGSP 47182 from Y76	812
	796	pers. obs.	extrapolated from m2 1956 II 371	[389]
	1,185	pers. obs.	M1 1956 II 364	
	1,511	pers. obs.	M2 1956 II 364	
<i>Protaceratherium</i>	130	Ginsburg et al. (1992)	M3 Hang Mon (Vietnam)	153
sp.	175	pers. obs.	extrapolated from cuboid Pak 1876	[32]
<i>Plesiaceratherium</i>	459	pers. obs.	M2 Pak 1042	
<i>naricum</i>	488	pers. obs.	Astragalus Pak 1142 (min)	
	525	pers. obs.	M3 Pak 1042	554
	600	pers. obs.	Astragalus Pak 1683 (max)	[97]
	699	pers. obs.	extrapolated from m2 Pak 1661	
<i>Pleuroceros</i>	694	pers. obs.	Astragalus Pak 1139 (min)	
<i>blanfordi</i>	815	pers. obs.	Astragalus Pak 1138 (max)	
	922	pers. obs.	M3 Pak 1013 (min)	

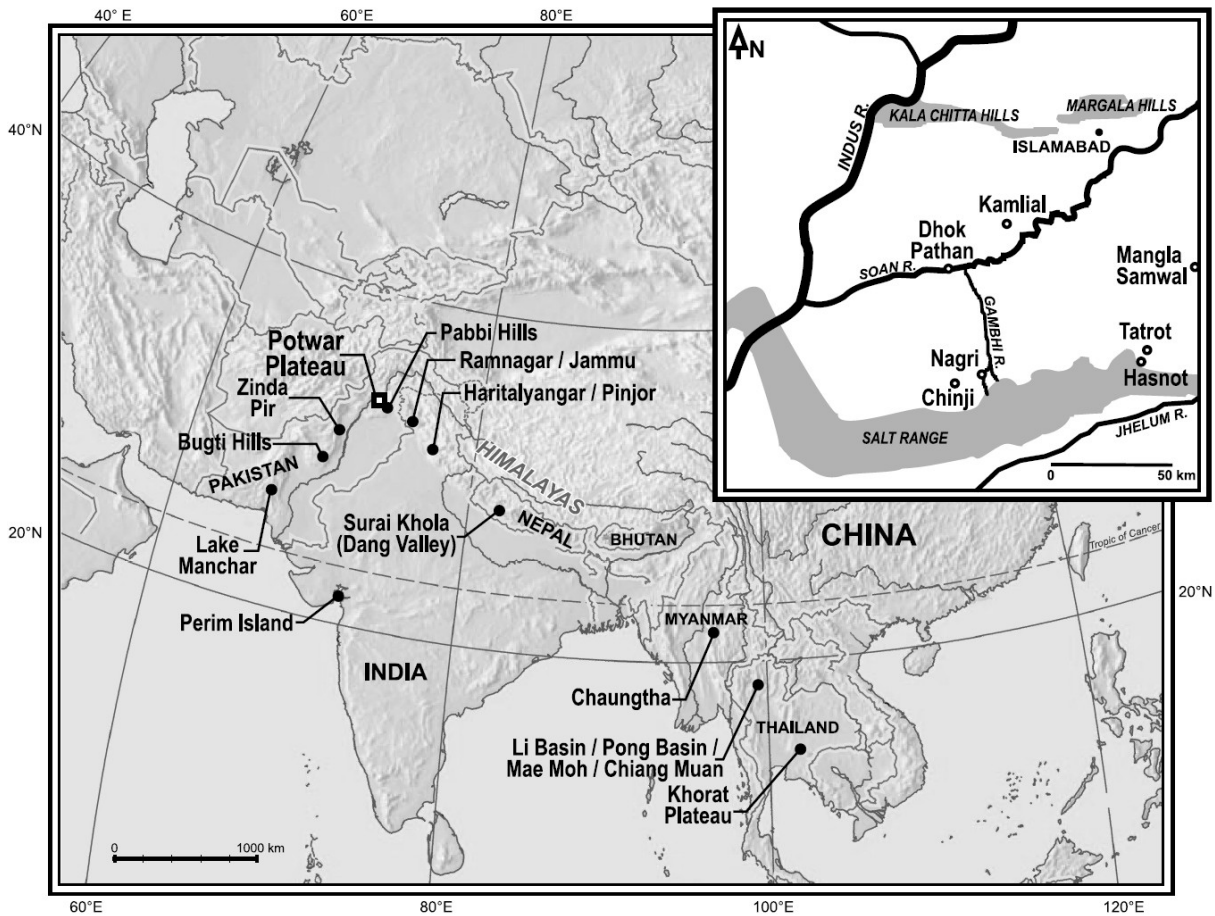
	1,254	pers. obs.	M3 Pak 918 (max)	
	1,267	pers. obs.	m1 Pak 1038 (min)	1,525
	1,398	pers. obs.	m1 Pak 1038 (max)	[725]
	1,762	pers. obs.	M1 Pak 1061 (min)	
	1,916	pers. obs.	M2 Pak 1019 (min)	
	2,144	pers. obs.	M2 Pak 760 (max)	
	3,081	pers. obs.	M1 Pak 1012a (max)	
<i>Mesaceratherium</i>	871	pers. obs.	Astragalus Pak 1136 (min)	
<i>welcommi</i>	1,341	pers. obs.	m1 Pak 1023 (min)	
	1,406	pers. obs.	Astragalus Pak 1134 (max)	
	1,412	pers. obs.	M3 Pak 1051 (min)	1,615
	1,479	pers. obs.	M3 Pak 1032b (max)	[503]
	1,753	pers. obs.	m1 Pak 1054 (max)	
	2,265	pers. obs.	M2 Pak 1032a (min)	
	2,390	pers. obs.	M2 Pak 2203 (max)	
<i>Alicornops</i>	542	Cerdeño & Sanchez (2000)	Astragalus of <i>A. simorreense</i> (min)	
<i>cf. simorreense</i>	728	Cerdeño & Sanchez (2000)	m1 of <i>A. simorreense</i> (min)	875
	909	Cerdeño & Sanchez (2000)	Astragalus of <i>A. simorreense</i> (max)	[333]
	1,321	Cerdeño & Sanchez (2000)	m1 of <i>A. simorreense</i> (max)	
<i>Alicornops</i>	515	Heissig (1972)	Astragalus NG 349	
<i>complanatum</i>	787	Heissig (1972)	m1 1956 II 393 (min)	821
	1,162	Heissig (1972)	m1 1956 II 392 (max)	[325]
<i>Brachypotherium</i>	1,859	pers. obs.	Astragalus Pak 1680 (min)	1,922
<i>gajense</i>	1,985	pers. obs.	Astragalus Pak 1872 (max)	[89]
<i>Prosantorhinus</i>	662	pers. obs.	Astragalus Pak 2126	
<i>shahbazi</i>	882	pers. obs.	extrapolated from m3 Pak 880	1,223
	1,465	pers. obs.	M2 Pak 1030	[556]
	1,884	pers. obs.	M1 Pak 1029	
<i>Brachydiceratherium</i>	1,118	pers. obs.	Astragalus YGSP 17757	1,905
<i>intermedium</i>	2,693	pers. obs.	extrapolated, m2 YGSP 24184f	[1,113]
<i>Brachydiceratherium</i>	1,224	Heissig (1972)	M3 CHJ 9 (min)	
<i>fatehjangense</i>	1,458	pers. obs.	Astragalus Pak 183 (min)	
	1,512	pers. obs.	Astragalus CHC 10 (max)	
	1,730	pers. obs.	M3 Pak 1012c (max)	1,999
	1,972	pers. obs.	M2 Pak 2207	[633]

	2,433	pers. obs.	M1 Pak 878	
	2,724	pers. obs.	m1 Pak 1069 (min)	
	2,943	pers. obs.	estimated from m1 Pak 1446 (max)	
<i>Brachypotherium</i>	1,534	Heissig (1972)	M1 1956 II 439 (min)	
<i>perimense</i>	1,619	Heissig (1972)	M3 CHO 6 (min)	
	2,028	Heissig (1972)	M2 1956 II 438 (min)	
	3,291	pers. obs.	M3 CCZ RH 22 (Thailand) (max)	
	3,747	pers. obs.	Astragalus YGSP 21109 (min)	3,712
	4,263	Heissig (1972)	M1 1956 II 448 (max)	[1,581]
	4,464	pers. obs.	Astragalus from Thailand (max)	
	4,662	Heissig (1972)	M2 1956 II 460 (max)	
	5,413	pers. obs.	m1 Y50554 (min)	
	6,097	pers. obs.	m1 from Thailand (max)	
<i>Gaindatherium</i>	726	pers. obs.	m1 Pak 1659	810
<i>cf. browni</i>	894	pers. obs.	extrapolated from p4 Pak 1660	[119]
<i>Gaindatherium</i>	627	Heissig (1972)	M1 1956 II 241 (min)	
<i>browni</i>	635	Heissig (1972)	M3 1956 II 241 (min)	
	716	Heissig (1972)	M3 1956 II 241 (max)	
	841	Khan et al. (2014)	m1 PUPC 11/101 (min)	
	871	Heissig (1972)	Astragalus CHD 4 (min)	1,069
	882	Heissig (1972)	M2 1956 II 241 (min)	[449]
	1,257	Heissig (1972)	Astragalus 1956 II 331 (max)	
	1,419	Khan et al. (2014)	M2 PUPC 09/58	
	1,431	Heissig (1972)	m1 1956 II 247 (max)	
	2,013	Heissig (1972)	M1 CHK 6 (max)	
<i>Gaindatherium</i>	492	Heissig (1972)	M3 NG 351	
<i>vidali</i>	627	Heissig (1972)	M1 NG 350	
	909	pers. obs.	Astragalus YGSP 47077 (min)	829
	953	Heissig (1972)	m1 1956 II 260	[268]
	1,163	Heissig (1972)	Astragalus CHD 3 (max)	
<i>cf. Rhinoceros</i>	1,209	pers. obs.	Astragalus Pak 1458 (min)	
<i>sp.</i>	1,257	pers. obs.	Astragalus YGSP 47266 (max)	1,738
	1,831	pers. obs.	extrapolated from m1 Pak 171A	[673]
	2,654	pers. obs.	M2 YGSP 17538	
<i>Dicerorhinus</i>	803	pers. obs.	M3 YGSP 28100	
<i>aff. sumatrensis</i>	1,248	pers. obs.	M1 YGSP 28100 (min)	1,232

	1,645	pers. obs.	M1 YGSP 28100 (max)	[421]
<i>Ceratotherium</i>	1,619	pers. obs.	M3 YGSP 17993	
<i>neumayri</i>	2,469	Antoine & Saraç (2005)	Astragalus AK5-634 (min)	2,487
	3,373	Antoine & Saraç (2005)	Astragalus AK5-423 (max)	[877]

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558



559

560 **Fig. 18.1.** Location map of the main rhinocerotid-yielding areas discussed in the text (Pakistan,
 561 India, Nepal, Bhutan, Thailand, and Myanmar), with special emphasis on the Potwar Plateau
 562 (detailed at top right). After West et al. (1978), Pilbeam et al. (1979), Nanda (2002), Chavasseau
 563 et al. (2006), and Antoine et al. (2013).

564

565

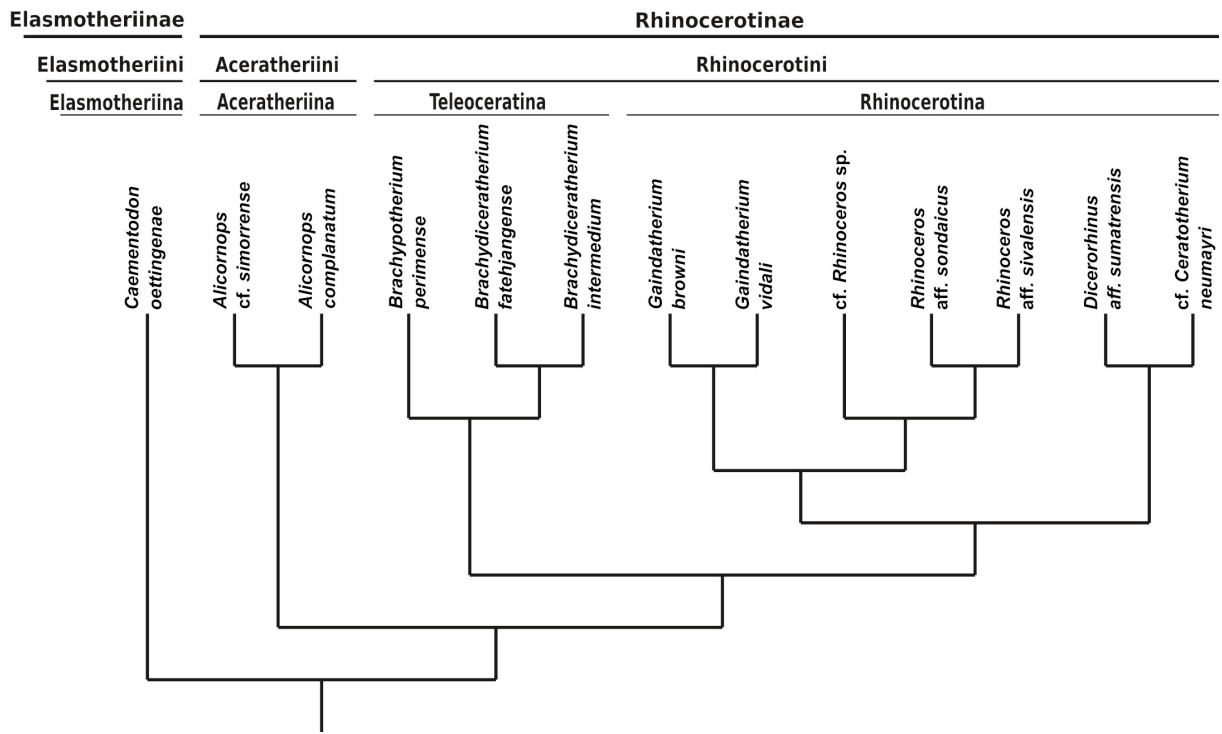
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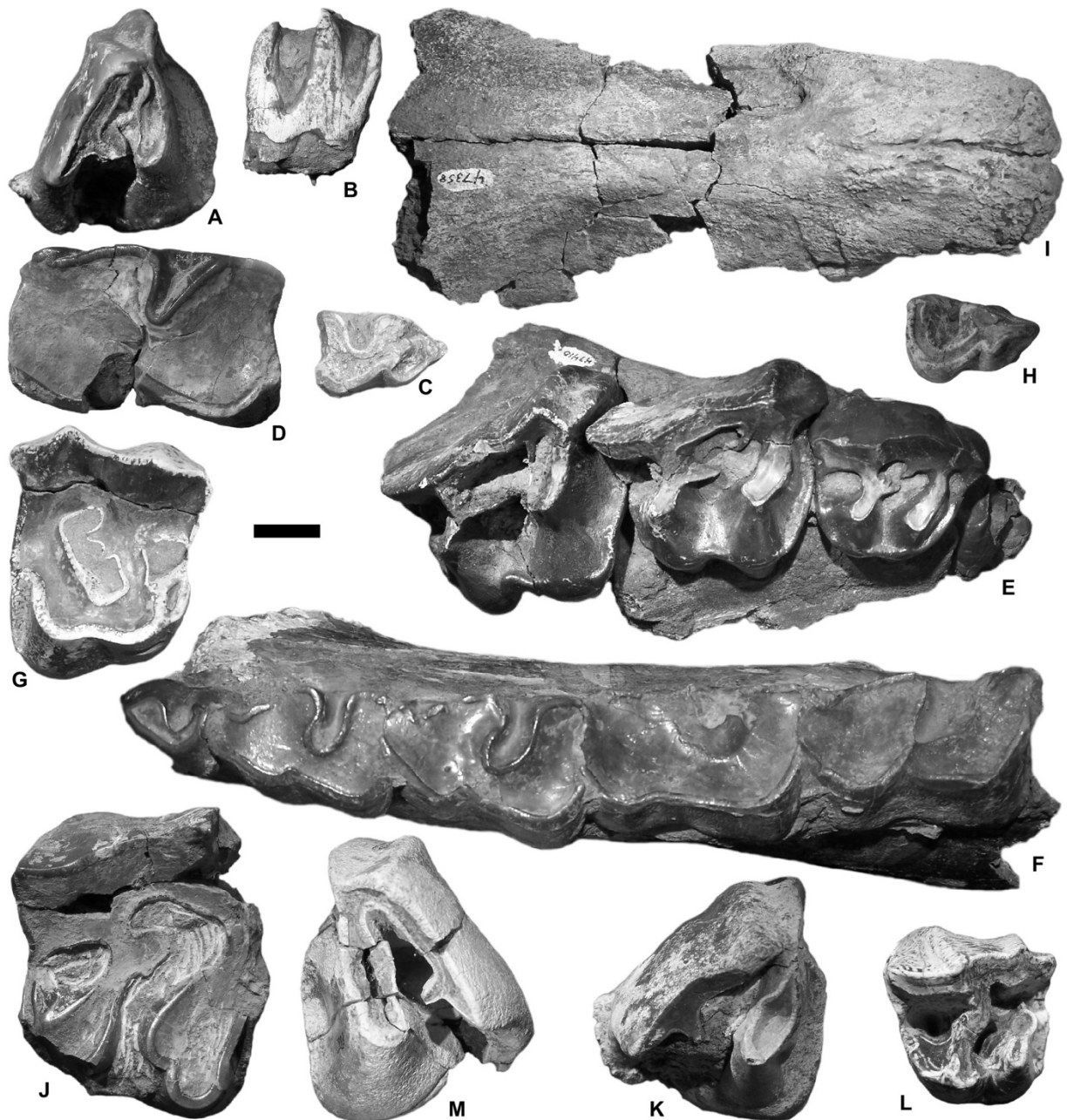
Rhinocerotidae



570

571 **Fig. 18.2.** Informal phylogenetic relationships of rhinocerotids from the Siwalik faunal
 572 sequence of the Potwar Plateau. Phylogenetic framework follows Antoine et al. (2010),
 573 Becker et al. (2013), and Sizov et al. (in press).

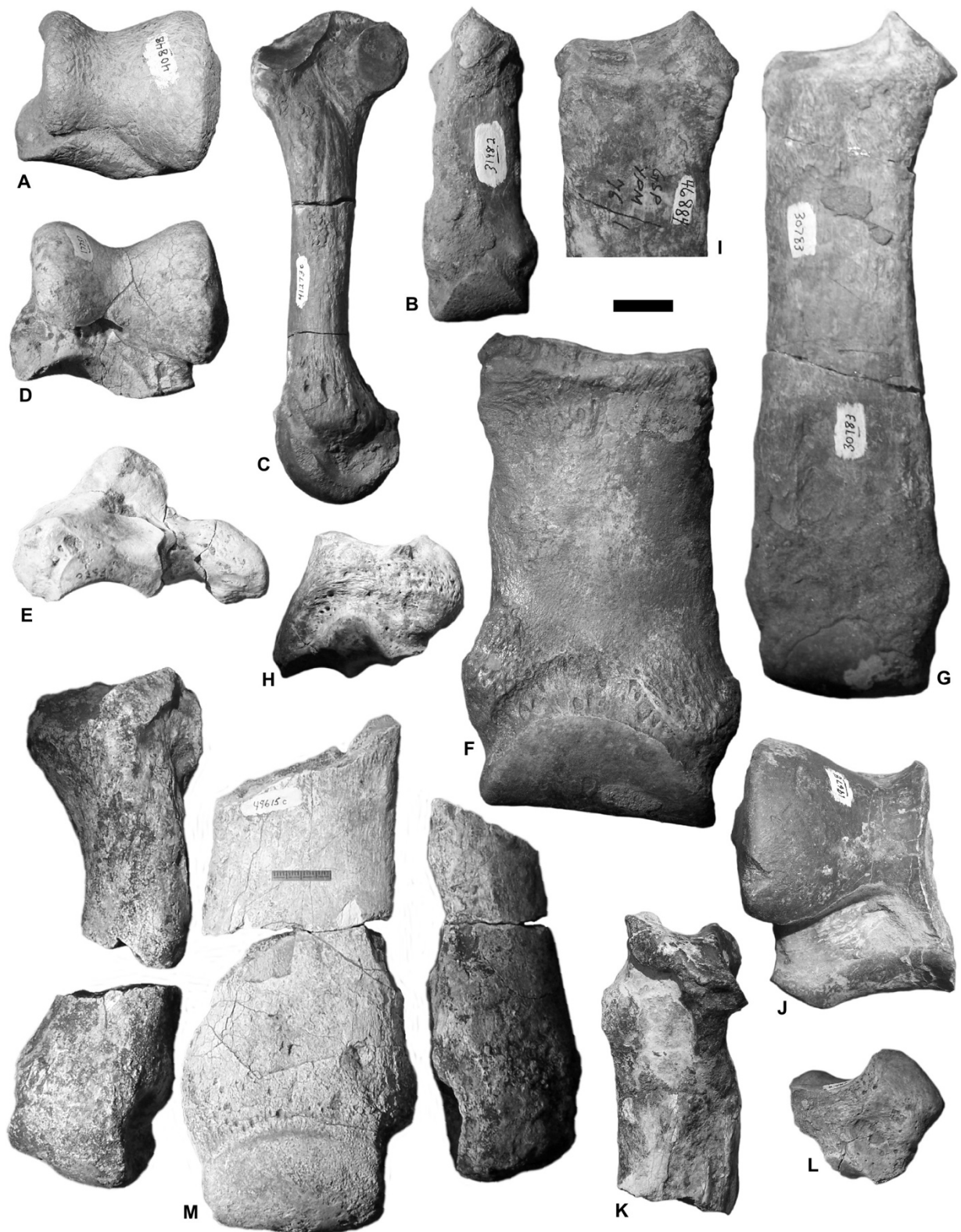
574



575

576 **Fig. 18.3** Rhinocerotid fossils from the Siwalik record of the Potwar Plateau: cranio-dental
 577 remains. **A-B.** *Caementodon oettingenae* Heissig, 1972: right M3 (Y50690, Y942 locality), in
 578 occlusal view (A); left m1 (YGSP 47182, Y76 locality), in lingual view (B). Valleys are filled
 579 by cement. **C.** *Alicornops complanatum* (Heissig, 1972): right p2, in occlusal view (YGSP
 580 17960, Y504 locality). **D.** *Brachydiceratherium intermedium* (Lydekker, 1884): left m2, in
 581 occlusal view (YGSP 24184f, from Y678). **E.** *Brachydiceratherium fatehjangense* (Pilgrim,
 582 1910): juvenile right maxilla with D1-4, in occlusal view (YGSP 47140, Y496 locality). **F.**
 583 *Brachypotherium perimense* (Falconer & Cautley, 1847): left jaw with p2-m2, in occlusal
 584 view (YGSP 20609d, Y311 locality). **G.** *Gaindatherium browni* Colbert, 1934: left P4, in
 585 occlusal view (YGSP 26657, Y695 locality). **H.** *Gaindatherium vidali* Heissig, 1972: right p2,

586 in occlusal view (Y51741, Y1007 locality). **I.** *Gaindatherium* sp.: nasal bones, in dorsal view
587 (YGSP 47358, Y647 locality). **J.** cf. *Rhinoceros* sp.: right M1, in occlusal view (YGSP
588 17538, Y592 locality). **K.** *Rhinoceros* aff. *sivalensis*: right M3, in occlusal view (YGSP
589 28225, Y744). **L.** *Dicerorhinus* aff. *sumatrensis*: right P3, in occlusal view (YGSP 28099,
590 Y705 locality). **M.** *Ceratotherium neumayri* (Osborn, 1900): left M3, in occlusal view (YGSP
591 17993, KL008 locality). Scale bar = 15 mm (A-E, G, H, J-M) and 20 mm (F, I).
592



593

594 **Fig. 18.4.** Rhinocerotid fossils from the Siwalik record of the Potwar Plateau: postcranial
 595 remains. **A.** *Caementodon oettingenae* Heissig, 1972: left astragalus, in anterior view (YGSP
 596 40848, Y76 locality). **B.** *Alicornops complanatum* (Heissig, 1972): right Mt2, in anterior view
 597 (YGSP 31482, Y545 locality). **C-D.** *Brachydiceratherium intermedium* (Lydekker, 1884):
 598 right Mc4 (C), in medial view (YGSP 41273c, Y678 locality); left astragalus (D), in anterior

599 view (YGSP 17757, Y545). **E.** *Brachydiceratherium fatehjangense* (Pilgrim, 1910): right
600 magnum in medial view (YGSP 32536, Y738 locality). **F.** *Brachypotherium perimense*
601 (Falconer & Cautley, 1847): right third metatarsal, in anterior view (YGSP 22160, Y735
602 locality). **G-H.** *Gaindatherium browni* Colbert, 1934: left Mc3 (G), in anterior view (YGSP
603 30783, Y76 locality); right scaphoid (H), in medial view (Y50918, Y76 locality). To be
604 compared with the scaphoid of *Dicerorhinus* aff. *sumatrensis*. **I.** *Gaindatherium vidali*
605 Heissig, 1972: left Mc3, proximal fragment (YGSP 46884, Y76 locality), in anterior view. To
606 be compared with the Mc3 referred to as *G. browni*. **J.** cf. *Rhinoceros* sp.: right broken
607 astragalus, in anterior view (YGSP 19678, Y592 locality). **K.** *Rhinoceros* aff. *sivalensis*:
608 proximal fragment of a right Mc2, in posterior view (Y52781, Y980 locality). Note the
609 presence of a large trapezium-facet. **L.** *Dicerorhinus* aff. *sumatrensis*: right incomplete
610 scaphoid, in medial view (Y51445, Y76 locality). **M.** *Ceratotherium neumayri* (Osborn,
611 1900): right metacarpus (YGSP 49615, Y399 locality), in anterior view. Scale bar = 20 mm.
612

625 **Table 18.2.** Rhinocerotid species recognized in the Siwalik faunal sequence. Locomotor types
 626 are inferred through appendicular skeletal features. Diet (browser or mixed feeder) is
 627 hypothesized on the basis of tooth-crown height, amount of cement present, and
 628 morphological similarity with modern analogs. Body-weight range estimates result from the
 629 equations of Legendre (1989) and Fortelius & Kappelman (1993). BW, body-weight estimate,
 630 in kg; FLO, First Local Occurrence; LO, Last Local Occurrence; Loc., locality; N, number;
 631 pc, postcranial; spec., specimens.

Group	Species	Loc.	FLO	LLO	Loc.	N	N	Locomotion	Diet	Body
		FLO	(Ma)	(Ma)	LLO	spec.	Loc.			Weight
Elasmotheriina	<i>Caementodon oettingenae</i>	Y833	15.1	8.6	Y444	48	30	cursorial	mixed feeder	812
Aceratheriina	<i>Alicornops</i> cf. <i>simorrense</i>	Y478	14.1	14.1	Y478	1	1	cursorial	browser	875
Aceratheriina	<i>Alicornops complanatum</i>	Y802	16.8	8.0	Y547	33	8	cursorial	browser	821
Aceratheriina	<i>Alicornops</i> sp.	Y802	16.8	8.1	Y606	16	11	cursorial	browser	-
Teleoceratina	<i>Brachydiceratherium</i> <i>intermedium</i>	Y721	17.9	8.0	Y541	44	10	cursorial	browser	1905
Teleoceratina	<i>Brachydiceratherium</i> <i>fatehjangense</i>	Y747	17.9	7.4	Y382	44	29	graviportal	browser	1999
Teleoceratina	<i>Brachypotherium perimense</i>	Y739	18.0	7.2	KL15	180	62	graviportal	browser	3712
Rhinocerotina	<i>Gaindatherium browni</i>	Y692*	16.9	8.7	Y544	74	25	cursorial	browser	1069
Rhinocerotina	<i>Gaindatherium vidali</i>	Y501	14.1	8.0	Y1007	16	12	cursorial	browser	829
Rhinocerotina	<i>Gaindatherium</i> sp.	Y747	17.9	8.4	Y28	58	18	cursorial	browser	-
Rhinocerotina	cf. <i>Rhinoceros</i> sp.	Y744	16.7	16.0	Y592	9	2	cursorial	mixed feeder	1738
Rhinocerotina	<i>Rhinoceros</i> aff. <i>sondaicus</i>	Y311	10.1	10.1	Y311	1	1	cursorial	browser	~1500
Rhinocerotina	<i>Rhinoceros</i> aff. <i>sivalensis</i>	Y980	8.9	8.0	KL11	34	4	cursorial	mixed feeder	~2000
Rhinocerotina	<i>Dicerorhinus</i> aff. <i>sumatrensis</i>	Y641	13.7	10.1	Y311	10	5	cursorial	browser	1232
Rhinocerotina	<i>Ceratotherium neumayri</i>	Y399	8.0	7.4	Y907	6	3	cursorial	grazer	2487

632 *The age of locality Y692 is not well-constrained. Current estimates range from 16.5 to 17.3
 633 Ma; the midpoint is used here.